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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE
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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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The *Fishery Bulletin* (USPS 090-870) is published quarterly by Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Bin C15700, Seattle, WA 98115. Second class postage paid to Finance Department, USPS, Washington, DC 20260.

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The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 31 March 1982.

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For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402—Subscription price per year: $14.00 domestic and $17.50 foreign. Cost per single issue: $4.00 domestic and $5.00 foreign.

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THE SPAWNING ENERGETICS OF FEMALE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

J. ROE HUNTER AND RODERICK LEONG[1]

ABSTRACT

The seasonal pattern in incidence of postovulatory follicles in northern anchovy females indicated that they spawn about 20 times per year. The maturation rates of females in the laboratory indicated that they were capable of maturing a spawning batch of eggs at weekly intervals. Examination of the egg size frequency distributions in sea-caught specimens indicated that vitellogenesis and egg maturation continued until the last spawning. We evaluated for northern anchovy the fat-water balance, caloric values of tissues, annual fat cycle, seasonal changes in egg weight, total calories present in a mature ovary, batch fecundity; and determined in the laboratory the gross caloric conversion efficiency (12.8%). These measurements indicated that the caloric equivalent of only two spawning batches are present in a mature ovary at any time and that two-thirds of the annual cost of 20 spawnings could be supplied by fat stores. Estimates of annual reproductive effort (egg calories/ration calories × 100) ranged from 8% for 1 year to 11% for 3-year-old females. A daily ration of copepods equivalent to 4-5% of female wet weight per day is required to support the annual cost of growth and reproduction.

Histological evidence indicated that female northern anchovy, *Engraulis mordax*, spawned about once a week in February 1978 (Hunter and Goldberg 1980) and at 7-10 d intervals from late January through the middle of April 1979 (Hunter and Macewicz 1980). Egg and larva survey data indicate that some spawning occurs throughout the year, although about 50% of the annual production of northern anchovy larvae occurs during the peak months of spawning (February to April) (Lasker and Smith 1977). These findings indicate that northern anchovy females spawn many times per year. Thus, the annual fecundity of northern anchovy is higher than originally suspected by MacGregor (1968) and may be regulated by availability of food. Energy regulation of fecundity has been suggested for other marine fish stocks and could be important as a density-dependent population regulation mechanism (Bagenal 1973).

The objectives of this study were: to validate recent work on northern anchovy spawning by determining if such a high frequency of spawning is developmentally and energetically possible; to estimate the annual energy cost of reproduction; and to discuss the sources of variation. We estimated the average number of spawnings by northern anchovy females in a year and tested the hypothesis that they are capable of maturing eggs at the required rate. We considered the energy cost of reproduction, factors that affected variation in costs, and related reproductive costs to fat stores. Finally we estimated the annual reproductive effort (egg cal/ration cal). In addition to data collected specifically for this study, we used data available at the Southwest Fisheries Center (SWFC), La Jolla, Calif., including many unpublished sources.

METHODS

Field Data

To estimate the annual number of spawnings by northern anchovy, we used the data of Hunter and Goldberg (1980) and Hunter and Macewicz (1980) on the incidence of 24-h-old postovulatory follicles. The proportion of mature females with 24-h-old postovulatory follicles was considered equivalent to the fraction of females spawning per day during a cruise (Hunter and Goldberg 1980). All samples were taken in the Southern California Bight in 1977-79; the number of females analyzed per cruise was 148 from March 1977; 14 from September 1977; 295 from February 1978; 395 from January-February 1979; 557 from March-April 1979; and 33 from June 1979. Data were plotted at the mid-date for the cruises which were 10-22 d long.

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

Manuscript accepted October 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

To estimate the rate of egg maturation required for weekly spawning, we used the frequency distributions of egg size in mature northern anchovy ovaries of females taken at sea. We measured distributions in 10 females taken in the Southern California Bight in February 1979, and in 6 taken in Monterey Bay in March 1979 by Hunter and Macewicz (1980). Five of the females from the Southern California Bight had 24-h-old postovulatory follicles indicating spawning had occurred on the day before they were captured, and the other five were mature without evidence of recent spawning. The ovaries of the six females from Monterey were highly atretic and in post-spawning condition, but had yolked eggs (Hunter and Macewicz 1980). This latter group was used to illustrate the condition of ovaries at the cessation of spawning. Our method of measuring the egg size-frequency distributions was similar to that of MacGregor (1968). We counted and measured to the nearest 0.05 mm all eggs >0.05 mm (major axis) in a weighed sample of the ovary.

Seasonal changes in fat content of female northern anchovy were calculated using the original data summarized by Lasker and Smith (1977). Their samples were taken at roughly monthly intervals from February 1965 to June 1967 (n = 593). Their data, supplemented by additional data (n = 338) taken in the summer and fall of 1979, were used to estimate the relation between wet weight without gonad (W) and fat content (F) and dry weight (without fat) (D). The multiple regression equation for this relation was

$$W = -0.018 + 0.320\,F + 5.469\,D \qquad (1)$$

where all variables are in grams, r^2 = 0.969, and n = 981. This equation permitted calculation of wet weight of northern anchovy females after fat gain or loss. Wet weight changes only slightly with fat loss because water content increases as fat decreases (Iles and Wood 1965) (Table 1). The same data were used to establish the relation between dry weight (without fat) (D) and standard length (L) where

$$\log_{10} L = 0.313 \log_{10} D + 1.930, \qquad (2)$$

r^2 = 0.974. Thus, wet weight can be estimated for northern anchovy of any standard length given the fat content.

Ahlstrom[2] measured the major and minor axes of 50-150 northern anchovy eggs taken in each of 58 standard ichthyoplankton tows (Smith and Richardson 1977) along the coast of California and Baja California in 1955, 1956, 1957, and 1965. These data, combined with an additional 30 tows (100 eggs measured/tow) taken in the same region in 1969, were used to estimate seasonal changes in the size of northern anchovy eggs. We calculated monthly mean egg dimensions for the combined data; number of tows per month varied from 9 to 16 (February-July) and from 1 to 4 in the period of low egg abundance (August-December). We calculated the mean volume of the eggs per month from average egg dimensions using the equation for a prolate spheroid. The volume (V) in cubic millimeters was converted to dry weight (E) in milligrams with the relation established in the laboratory using freshly spawned eggs

$$E = 0.0012 + 0.0930\,V \qquad (3)$$

where r^2 = 0.646 and n = 32.

Laboratory Data

Three groups of northern anchovy of 1,200-1,300 fish each were matured in the laboratory to measure the rate of ovarian maturation and to estimate gross growth efficiency. The fish were

[2] E. H. Ahlstrom, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, unpubl. data, 1979.

TABLE 1.—Relationship between fat-free dry weight or length and wet weight for northern anchovy at the average seasonal minimum and maximum fat content. Relationships calculated from regressions; all body weights are without gonads.

Standard length[1] (mm)	Fat-free dry weight (g)	Wet weight and water content at minimum (15%)[2] fat content			Wet weight and water content at maximum (41%)[2] fat content		
		Fat (g)	Wet weight[3] ± 95% C.I.	Water[4] (%)	Fat (g)	Wet weight[3] ± 95% C.I.	Water[4] (%)
106	2.000	0.353	11.03 ± 0.19	79	1.390	11.36 ± 0.11	70
118	2.891	0.510	15.96 ± 0.13	79	2.009	16.44 ± 0.18	70
131	4.000	0.706	22.08 ± 0.12	79	2.780	22.75 ± 0.35	70

[1] From Equation (2) in text.
[2] Percentage of the dry weight including fat.
[3] From Equation (1) in text; 95% confidence intervals calculated using Gauss multipliers (Snedecor and Cochran 1967).
[4] $[W - (D + F)/W] \times 100$, where W = wet weight without ovary, D = fat-free dry weight, and F = weight of fat.

purchased from bait dealers from September to October in 1977 and 1978 and held in circular tanks 4.6 m in diameter × 1 m deep (volume 16.6 m^3) with a fresh seawater inflow of 20 l/min. The fish were exposed to the natural photoperiod but were shielded from direct sunlight. They were fed a ration of Oregon Moist Trout Pellets[3] 6 d/wk. The pellets were dispensed with an automatic feeder over a 4-5 h feeding period beginning at 0800 h (Leong 1971).

To estimate the rate of egg maturation (group 1), 8-12 females were sampled twice weekly for 6 wk. The ovaries of nearly all females were immature (no yolked oocytes) when sampling began; the mean standard length (SL) of females was 112.4 mm increasing to 116.4 mm in 6 wk. The fish were held at ambient temperatures which ranged from 17.9° to 22.0° C and averaged 19.7° C; daily temperatures closely followed those taken at the Scripps Institution of Oceanography pier. We measured standard length, wet weight, and determined the frequency distribution of egg sizes within the ovary for each female sampled. We used as a measure of the state of sexual maturity, the mean size of eggs (major axis) within the most advanced spawning batch. The number of eggs within a batch was calculated from the wet weight of the female using the batch fecundity equation of Hunter and Macewicz (1980)

$$\log_e T = 4.248 + 1.620 \log_e W. \qquad (4)$$

(Equation corrected for bias in taking the antilog; Beauchamp and Olson 1973), where T = total number of eggs in a spawning batch and W = female wet weight (without ovary) in grams.

To measure growth efficiency, two groups (groups 2 and 3) were held under similar tank conditions, but were sampled at 2-wk intervals beginning at the end of November and ending in mid-February. Group 2 was in captivity for about 1 mo and group 3 for 2 wk prior to sampling. Group 2 was held at 15.6° C while group 3 was held at ambient temperatures which ranged from 15.2° to 17.0° C and averaged 16.0° C. Mean standard length of fish in groups 2 and 3 was 107.2 mm at the beginning and 121.4 mm at the end of the experiment.

The stomach contents of each fish sampled from groups 2 and 3 were weighed and used to determine the mean ration for the experiment. The ration was calculated from the equation

$$R = r \cdot s \cdot t + S_e \qquad (5)$$

where R = ration, expressed as wet weight food consumed/wet weight fish (in grams); r = rate of gastric evacuation (dashed line, Figure 1); s = average weight of food in stomach/fish weight during the period of gut filling (solid line, Figure 1); t = duration of feeding (4 h, group 2; 5 h, group 3); and S_e = weight of food in stomach/fish weight

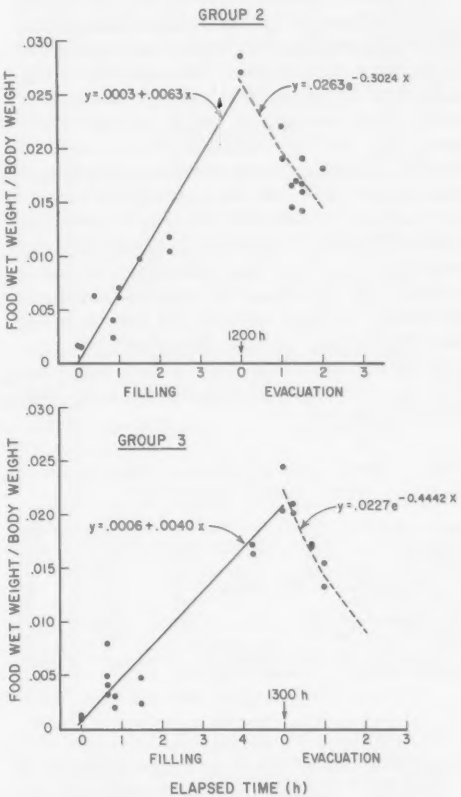

FIGURE 1.—Rate of stomach filling and gastric evacuation in two groups of northern anchovy fed Oregon Moist Trout Pellets. Weight of stomach contents expressed as a proportion of fish weight; each point is mean for 8-12 fish; feeding began at 0 h (filling) and ended at 0 h (evacuation) (arrow); time of day when feeding ended is above arrow. Daily ration calculated from these data was 4.4% body weight/d, group 2; and 4.6% body weight/d, group 3.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

at end of feeding period. Similar functions have been used by Tyler (1970), discussed and used by Eggers (1977), and discussed by Elliot and Persson (1978). The daily pattern of feeding and evacuation and the data used to calculate the parameters for the ration equation are given in Figure 1. We use an exponential equation to estimate rate of gastric evacuation (r) because it is required by theory and the above model and use a linear regression equation for gut filling because the equation is used only to provide an empirical estimate of the mean stomach contents (s) during feeding.

The mean ration for a feeding day was 0.0437 g/g body wet weight (group 2) and 0.0462 g/g body wet weight (group 3); these values were multiplied by the mean wet weight of fish sampled (18.6 g, group 2; 17.6 g, group 3) to express the ration in terms of the average fish weight in each experiment. This value was adjusted by the ratio, total number of feeding periods/duration of the experiment (days) (ratio = 59/69, group 2; 67/78, group 3), to adjust the ration for days when no feeding occurred. This daily ration for the experiment was converted to calories by multiplying by 0.656 (average ratio of dry to wet weight for stomach contents of northern anchovy fed Oregon Moist Trout Pellets) and by 4,912, the caloric value per gram for this food (Table 2). The daily ration for fish in group 2 was 2,238 cal/d and was 2,245 cal/d for fish in group 3.

TABLE 2.—Mean calories per gram dry weight of various northern anchovy tissues and food.

Tissues or food	n	Mean calories	SD
Anchovy fat	4	9,227	40
Anchovy eggs (including fat)	4	5,450	90
Whole female anchovy, less ovary (fat free)	11	4,129	176
Anchovy ovary (fat free)	29	4,960	79
Anchovy ovary with 18%[1] fat	—	5,710	—
Oregon Moist Trout Pellets	4	4,912	214

[1] 18% is the mean fat content of northern anchovy ovaries; caloric value was calculated from the values for fat and fat-free ovary.

Dry weight and fat content of northern anchovy were determined for the first and last samples of groups 2 and 3. Fish were dried in an oven at 60° C until constant weight and fat extracted using Soxhlet extraction with chloroform-methanol (Krvarić and Mužinić 1950).

Caloric values of northern anchovy oil, newly spawned eggs, ovaries and whole females (without ovaries), and Oregon Moist Trout Pellets were estimated using a Parr bomb calorimeter and standard techniques (Table 2). Laboratory fish were used for all measurements except for the caloric value of northern anchovy oil where sea-caught specimens were used.

SPAWNING FREQUENCY AND RATE OF EGG MATURATION

Number of Spawnings per Year

We plotted the fraction of females spawning per day (females with 24-h-old postovulatory follicles) as a function of sampling date to estimate the number of spawnings produced by female northern anchovy in 1 yr. The seasonal change in the fraction of females spawning followed the seasonal change in the average relative larval abundance for 1953-60 (Lasker and Smith 1977) (Figure 2). The fraction of females spawning was the highest during peak spawning months and declined to zero by September. In peak spawning months the percentage of mature females spawning per day was 16-14%, indicating that individual females spawned every 6-7 d. The seasonal decline in the fraction of females spawning per day could be caused by an increase in the interval between spawnings in individual females, or by a complete cessation of spawning by an increasingly larger proportion of the population, or by a combination of these events.

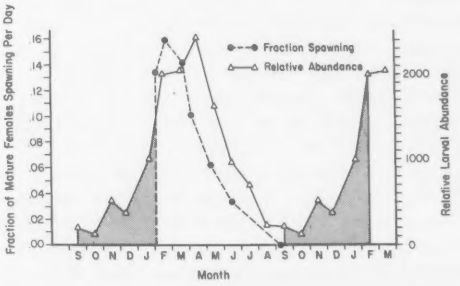

FIGURE 2.—Fraction of mature northern anchovy females from the Southern California Bight spawning per day during various months (dots). Fraction calculated from incidence of females with 24-h-old postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980). Triangles indicate relative larval abundance per month from 1953 to 1960 (Lasker and Smith 1977). Shaded areas indicate months where spawning fraction was not estimated; total spawnings per year by northern anchovy females was estimated from areas under the two curves (see text).

The area under the curve for fraction of females spawning per day is an estimate of the number of spawnings produced per female from February to September. This calculation indicated that each mature female northern anchovy spawned on the average 15 times between February and September. The number of spawnings that occurred in October-January (shaded area, Figure 2) had to be estimated indirectly because no ovary samples existed. We assumed that the number of spawnings was proportional to the relative larval abundance in October-January, adjusted by the ratio of the areas under the spawning fraction and larval abundance curves for Feburary to September. This calculation indicated that about five spawnings would have had to occur in October-January to account for the abundance of larvae in that period; this brings the total number of spawnings for female to 20 for the year.

Form of Frequency Distribution of Egg Size

The form of the egg size distribution in mature northern anchovy ovaries is illustrated for a female taken 24 h after spawning and a mature female without evidence of recent spawning (nonspawning) (Figure 3). Ovarian egg size distributions typically resemble these except for females with hydrated eggs, where the hydrated eggs stand out as a discontinuous group of large eggs. In mature females (without hydrated eggs) the egg size distributions are continuous and typically have one or two modes as illustrated. In the nonspawning female a major mode of large yolked eggs existed between 0.6 and 0.8 mm (major egg axis) and in the spawned female the first modal group occurred at about 0.5 mm. Eggs <0.2 mm are the most abundant size class in both ovaries. These small eggs, also abundant in immature ovaries, form part of the reservoir of immature unyolked eggs which are matured during each spawning season.

Yolk appears in the egg when the major axis of the egg reaches about 0.4 mm. The ovary of the spawned female (20.2 g) in Figure 3 contained 9,384 yolked eggs, whereas that of the nonspawning female (25.3 g) contained 26,761 yolked eggs. The batch fecundity equation (Equation (4)) predicts a batch size of 9,110 eggs for the spawned female and 13,120 eggs for the nonspawning female. Hence, about one spawning batch of yolked eggs existed in the spawned female and about two

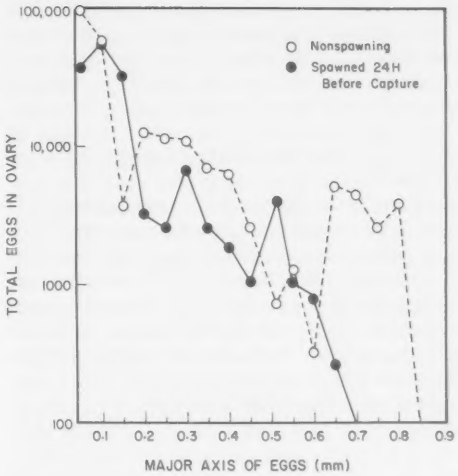

FIGURE 3.—Total eggs in ovary ($\log_{10}$ scale) as a function of the major egg axis for a 20.2 g female northern anchovy (ovary-free weight) captured 24 h after spawning and for a 25.3 g female, showing no evidence of recent spawning (nonspawning). Smallest eggs measured were 0.05 mm; measurements were made in increments of 0.05 mm. Females were captured in January to February 1979 in the Southern California Bight.

in the nonspawning female. If a female were to spawn more than a few times in one season, it would have to mature and yolk many of the small unyolked eggs in the ovary. If spawning were to occur at weekly intervals for months, this would be a continuous process.

Rate of Egg Maturation Required for Continuous Production of Eggs Compared With Laboratory Maturation Rate

For northern anchovy to continually mature and add yolk to a series of egg batches, the abundance of egg sizes in the ovary must vary inversely with the rate of egg maturation. Thus, a hypothetical curve for the rate of maturation of anchovy eggs can be constructed from the average size of eggs in each potential spawning batch within an ovary, if the time between batches or spawning frequency is known. This hypothetical rate can then be compared with the rate of egg maturation in the laboratory to determine if the predicted rate is possible.

To conduct this test for northern anchovy, we partitioned the total number of eggs in the ovary of 10 sea-caught fish into successive spawning

batches (starting with the largest eggs) and calculated the mean major axis of eggs in each successive batch. The number of eggs per batch was estimated from the wet weight of the females using the batch fecundity Equation (4).

As might be expected, the mean major axis of eggs in each of the potential spawning batches for the five females taken 24 h after spawning was about one spawning batch out of phase from the five nonspawning fish (Figure 4, upper). When the most advanced spawning batch of the recently spawned group was lagged by one spawning interval, the function was the same for both groups (Figure 4, lower) and similar to data on "nonspawning females" in Hunter and Goldberg (1980). The lower curves indicate that about four spawning batches of eggs >0.15 mm exist in the ovary of females near spawning condition. Hunter and Goldberg (1980) determined for 38 mature nonspawning females that the mean size of eggs in the most mature batch was 0.59 mm; and in the 5 females in the present analysis, the mean size was 0.71 mm. Thus a batch of eggs of 0.15 mm mean size major axis would have to reach about 0.6-0.7 mm in about 4 wk (28 d) if females were to spawn five or more times at weekly intervals.

The ovaries of all laboratory females were immature when the maturation experiment began (elapsed time = 0, Figure 5) although the mean size of eggs in the most advanced spawning batch was quite variable among females (mean egg size ranged from 0.13 to 0.48 mm). To illustrate the rate of ovarian maturation we used the average of the mean egg size in the spawning batch of individual females (Figure 5). The rate of maturation of ovaries in the laboratory group was similar to that predicted from egg size frequency distributions of wild fish, if one assumes spawning in the sea occurs weekly (line, Figure 5). The average of the mean size of eggs in the most advanced spawning batch was 0.15 mm after the first week of the experiment and was 0.62 mm 4 wk later. Thus maturation of eggs from 0.15 to 0.62 mm occurred in four wk and is about the same as the theoretical estimate based on egg size distributions in sea-caught specimens. This demonstrates that the rate of egg maturation required for continuous production of egg batches

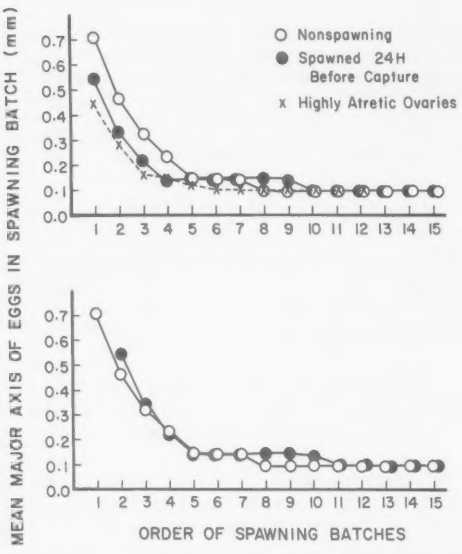

FIGURE 4.—Mean major axis of eggs in successive spawning batches within the ovary of northern anchovy. Number of eggs per batch estimated for each female from Equation (4). Numbers on abscissa indicate order of spawning batch with 1 = the most advanced batch. Circles are means of five nonspawning females (no evidence of recent spawning), and dots are means for five females having spawned within 24 h (females taken in the Southern California Bight); the X's are means for six females with highly atretic ovaries taken in Monterey Bay in 1979. The lower panel illustrates the correspondence between average egg size in successive batches in nonatretic ovaries when recently spawned females are lagged by one spawning batch interval. Only the 15 batches containing the largest eggs are shown.

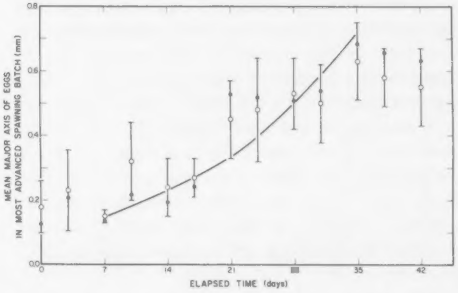

FIGURE 5.—Maturation of eggs in the most advanced spawning batch of laboratory-held northern anchovy as a function of elapsed time. Maturity is achieved when average egg size in batch attains 0.6-0.7 mm. Circles are averages of the mean size of eggs in the most advanced spawning batch of females sampled on a particular day, dots the median, and bars are ±2 SE. Number of eggs used to calculate the mean for each female was determined using Equation (4). The solid line is hypothetical maturation rate of egg batches from 0.15 mm (major egg axis), assuming females spawn at weekly intervals; the line is derived from data in Figure 4.

at 7-10 d intervals occurs in the laboratory and could occur in the sea. In addition, the forms of the theoretical and the laboratory maturation curves were similar, with maturation of small unyolked eggs being much slower than that of larger yolked eggs.

Cessation of Spawning

An assumption of some fecundity studies of multiple spawning fishes is that all eggs to be spawned in a season are yolked at the beginning of the season and spawning ends when these yolked eggs are depleted. The preceding analysis indicated that yolking of eggs from the reservoir of small unyolked eggs is a continuous process in northern anchovy. In this section we determined whether spawning ceases because of a lack of eggs of an appropriate size for maturation. We compared egg size-frequency distributions from six females with highly atretic ovaries with those of reproductively active females. Although the ovaries of the six females contained yolked eggs, they were highly atretic and judged to be in post-spawning condition, using histological criteria presented by Hunter and Macewicz (1980).

The form of the line relating the mean major axis of eggs to successive spawning batches (dashed line, Figure 4, upper) was similar in form to those of the other groups. The eggs in the most advanced spawning batch were smaller (0.45 mm) in atretic ovaries than in those of females that had spawned 24 h before capture (0.55 mm). Hunter and Goldberg (1980) showed that the mean major axis of the most advanced eggs (excluding hydrated eggs) was 0.46 mm in females captured on the night of spawning. This value is very close to the mean for highly atretic ovaries. Thus, oocyte maturation, at least in these six females, probably continued up to the time of the last spawning, whereupon maturation ceased and the remaining oocytes became atretic. Spawning did not cease because of lack of yolked eggs; the atretic ovaries of these six females had the same distribution of egg sizes as any female ovary immediately after spawning.

ENERGY COST OF SPAWNING

We consider here three variables affecting the cost of reproduction: Number of eggs in a spawning batch, size of eggs, and the energy existing in a mature ovary. Factors not considered include the metabolic costs of egg maturation and reproductive behavior and variation in the caloric content of eggs.

Number of Eggs

The spawning batch fecundity (number of hydrated eggs) of northern anchovy varies exponentially with female weight (Equation (4)). Similar to many other fishes (Bagenal 1973), fecundity among females of the same size or weight is highly variable. Variability may be caused by variations in egg size, food availability, and number of previous spawnings within the season.

Feeding conditions may not greatly affect batch fecundity in northern anchovy. Females matured in the laboratory (groups 2 and 3) were fed a high ration and grew about four times faster than those in the sea, yet the batch fecundity was about the same as field-caught specimens, which consume a lower ration (Table 3). Although the laboratory females had not begun spawning, their batch fecundity was similar to that of fish taken in the sea between January and April. This indicates that the average batch fecundity may not change over the first months of spawning. The fact that fecundity of females captured in March-April 1979 was about the same as that for January-February 1979 (Hunter and Macewicz 1980) also supports

TABLE 3.—Comparison of the batch fecundity of northern anchovy females matured in laboratory and in the sea within two weight classes.

Weight class (g)	Locality	*n*	Mean weight (without ovary) (g)	Batch fecundity (total eggs)	
				Mean ± 2 SE	Estimated for mean weight from fecundity equation for sea-caught female[1]
15-19.9	Laboratory[2]	38	17.9	8,910 ± 1,210	7,420
	Sea[3]	17	16.7	6,800 ± 1,150	6,690
20-24.9	Laboratory[2]	12	22.8	11,900 ± 950	11,100
	Sea[3]	21	22.6	10,400 ± 1,540	10,900

[1]From Equation (4) (Hunter and Macewicz 1980); intercept increased by 0.0647 ($\frac{1}{2}s^2$) to adjust for bias in taking antilog (Beauchamp and Olson 1973).
[2]Batch fecundity = number eggs in most advanced mode in ovary where mean egg size ≥0.65 mm (major axis; eggs not hydrated).
[3]Batch fecundity = number of hydrated eggs in females without new postovulatory follicles (Hunter and Goldberg 1980; Hunter and Macewicz 1980).

this view. We conclude that, at least over the first few months of spawning, the mean number of eggs per spawning batch may be independent of past spawning history.

Size of Eggs

The size of spawned northern anchovy eggs varies seasonally as do those of other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Smith and Richardson (1977) demonstrated that the major axes of northern anchovy eggs spawned in February 1972 were larger than those of eggs spawned in August 1972 ($P = 0.05$). The seasonal trend in dimensions of northern anchovy eggs is illustrated in Figure 6 (upper). The dry weight of eggs (calculated from their volume (Equation (3)) varies by about 20% over the spawning season; thus, females could produce about five more spawnings/yr at the minimum egg size than at the maximum with no increase in energy demand. The seasonal trend in egg dry weight is similar to the relative larval abundance (shaded area of Figure 6), with the largest eggs produced in February to April when most of the spawning occurs and the smallest eggs late in the summer when the least spawning occurs. Several possible explanations exist for the seasonal trend in egg size. Females may produce smaller eggs as the spawning season progresses or, alternatively, large females which begin spawning earlier may produce larger eggs than small females. Regardless of the mechanism, it probably is adaptive to produce larger eggs early in the spawning season when water temperatures are cooler since the advantage falls to larger eggs as water temperature declines, because incubation periods are longer (Ware 1975).

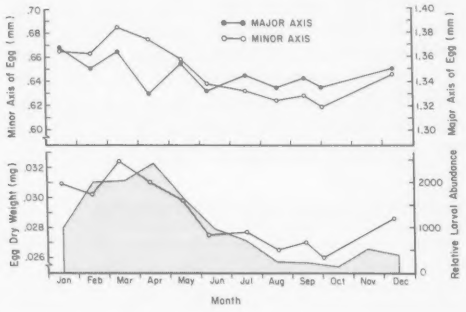

FIGURE 6.—Mean size of northern anchovy eggs taken in routine plankton tows by month. Upper, mean major and minor axes of eggs; lower, mean weight of eggs calculated from average dimensions of eggs given in upper figure using Equation (3); shaded area is the relative larval abundance for years 1953-60, from Lasker and Smith (1977).

Maturation of Eggs

Northern anchovy eggs < 0.1 mm are spherical; they become oblate spheroids between 0.1 and 0.25 mm (major axis) and thereafter retain the same proportionality between axes through hydration and spawning (Figure 7, upper). Hydration of the spawning batch of eggs (rapid uptake of fluid) begins about 12 h before spawning (Hunter and

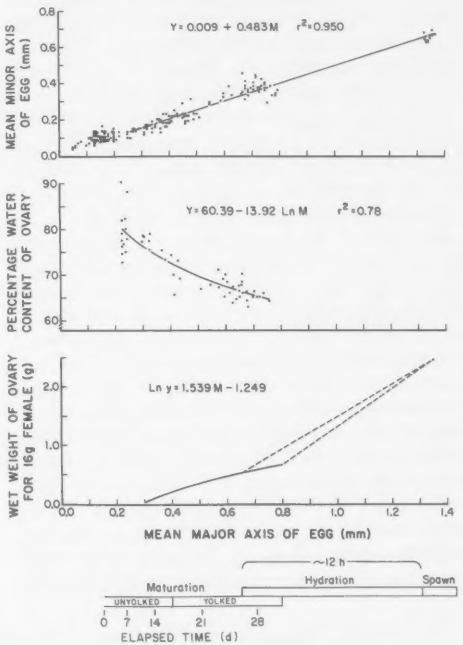
MEAN MINOR AXIS OF EGG (mm)
Y = 0.009 + 0.483 M r²=0.950
PERCENTAGE WATER CONTENT OF OVARY
Y = 60.39 − 13.92 Ln M r²=0.78
WET WEIGHT OF OVARY FOR 16g FEMALE (g)
Ln y = 1.539 M − 1.249
MEAN MAJOR AXIS OF EGG (mm)
~12 h
Maturation
Hydration
Spawn
UNYOLKED
YOLKED
ELAPSED TIME (d)

FIGURE 7.—The mean length of the minor egg axis (upper), water content of the ovary (middle), and ovary wet weight of a 16 g northern anchovy female calculated from Equation (6) (bottom), as functions of the mean major egg axis of eggs in the most advanced spawning batch (natural logarithms were used). Original data for Equation (6) (solid line, bottom) given in Hunter and Goldberg (1980); dashed lines indicate the range of egg sizes that may hydrate; and they converge at the average weight of a hydrated ovary in a 16 g female. Time scale on abscissa is based on hypothetical rate of egg maturation required for weekly spawning (see Figure 4).

Macewicz 1980), resulting in a rapid increase in ovary wet weight (Figure 7, lower) but no change in dry weight (Le Clus 1979). The mean size of eggs in a spawning batch, just before hydration, ranges from 0.6 to 0.8 mm; eggs >0.8 mm nearly always show histological signs of hydration. The average size of eggs that are hydrated would be expected to vary since the size of spawned eggs is variable.

The wet weight of the ovary (G) increases during maturation and is a function of the mean major axis of the eggs in the most mature spawning batch (M) and female wet weight without ovary (W); in northern anchovy this function is expressed as

$$\log_e G = -4.213 + 1.069 \log_e W + 0.555\, M \log_e W \qquad (6)$$

(Hunter and Goldberg 1980) (Figure 7, lower). The water content of the ovary of laboratory females (group 1) declined during maturation from 80 to 65% just before hydration (Figure 7, center). The fat content did not change significantly over the maturation period; mean ovarian fat content of laboratory-matured northern anchovy was 18.6±1.2% (±2 SE of mean, n = 41) of ovary dry weight. As the fat content did not change, the caloric value of ovarian tissue can be considered to be constant at 5,710 cal/g dry weight (Table 2).

Using Equation (6), caloric values (Table 2), and water content of ovary (Figure 7), we estimate the ovary of a 16.4 g female contains 933 cal just after spawning when the mean major axis of most advanced eggs = 0.46 mm (Hunter and Goldberg 1980). The spawning batch of a 16.4 g female contains 6,500 eggs or 1,066 cal (from Equation (4)). Thus, just before spawning the ovary contains about 2,059 cal and the most advanced spawning batch constitutes about 52% of the calories in the ovary (documentation given in Table 4). Similar calculations can be made using the volume of eggs in the ovary and egg dimensions given in Figure 7 (upper) or by calculating the wet weight of the ovary at 0.46 mm egg major axis (after spawning) and at 0.81 mm egg major axis (at onset of hydration) using Equation (6). All calculations yield similar results when converted to dry weight or calories, i.e., about one-half of the calories in the ovary are lost in one spawning. We conclude that the calories invested in a mature ovary are small relative to the total reproductive cost of 20 spawnings.

ANNUAL FAT CYCLE AND SPAWNING

As the caloric equivalent of only two spawnings exists in the ovary at one time, northern anchovy must use energy stored in other tissues and food income to support reproduction. Lasker and Smith (1977) showed that the fat content of northern anchovy, like many other clupeoids (Blaxter and Holliday 1963; Shul'man 1974) varies seasonally. The fat accumulates in the body rapidly between April and July, matching the annual spring bloom of zooplankton (Lasker and Smith 1977). It usually remains high through December and then declines to a minimum between February and May (Figure 8). The decline in fat occurs during the months of maximum spawning. Thus, fat stored

TABLE 4.—Reproductive characteristics for the average female northern anchovy.

Item	Value	Explanation and data source
Weight and fecundity:		
Mean female wet weight, less ovary	16.4 g	For 1978 and 1979 (Hunter and Macewicz 1980)
Ovary wet weight after spawning[1]	.601 g	Equation (6) where M = 0.46 mm
Ovary dry weight after spawning[1]	.174 g	Percentage water in ovary from Figure 7 (center)
Number of eggs in one spawning batch	6,500 eggs	Equation (4)
Number of eggs spawned/yr	130,000 eggs	Assume 20 spawnings (Figure 2)
Dry weight one spawned egg	.0301 mg	Mean of monthly dry weight: (Figure 6) weighted by relative monthly larval abundance (Lasker and Smith 1977)
Caloric content of ovaries and spawn:		
Calories in one spawning batch	1,066 cal	Caloric value of eggs = 5,450 cal/g (Table 2)
Calories in ovary after spawning	993 cal	Caloric value of ovary = 5,710 cal/g (Table 2)
Calories in ovary just before spawning	2,059 cal	
Percentage of calories in ovary lost in one spawning batch	52%	
Daily spawning cost during peak spawning months	152 cal/d	Assume spawning interval = 7 d
Spawning related to fat stores:		
Maximum fat in body	2.009 g	Equation (1) where 41% of dry weight = fat
Minimum fat in body	.510 g	Equation (1) where 15% of dry weight = fat
Total fat stores	13,831 cal	Caloric value of fat = 9,227 cal/g (Table 2)
Fat stores in spawning batch equivalents	13 batches	

[1] Females with postovulatory follicles < 24 h old.

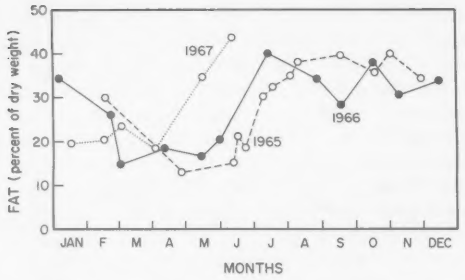

FIGURE 8.—Annual fat cycle of northern anchovy. Fat content expressed as a percentage of dry weight for various months in 1965, 1966, and 1967. Data from Lasker and Smith (1977).

from the previous spring and summer may be used the following year to support reproduction. Fat stores may not be used directly to promote egg production, which are largely protein, but rather to provide energy needed for metabolism, permitting energy from food to be used for egg maturation.

We calculated the number of spawnings that could be financed by the annual decline in fat stores, assuming that this energy or its equivalent is used for reproduction. We used the average minimum and maximum fat level for the 3 yr (Table 5) to estimate the grams of fat annually available for reproduction. Using the dry weight, fat, and wet weight relation (Equation (1)), we calculate that a 16.4 g female would store annually 13,831 cal of fat (Table 4) which is equivalent to 13 spawning batches. Thus, about two-thirds of the annual cost of egg production can be accounted for by the annual decline in fat stores.

The rate of increase in fat in the spring was similar in the 3 yr (1965-67) although the timing of the onset varied by 2-3 mo. The maximum rate occurred in the late spring or summer over a period of about 63 d (Table 5). Nearly all fat stores were accumulated over this period; on the average fat increased from 16.5 to 40.5% of the dry weight over the 63 d. Thus, calories would accumulate in a 16.4 g fish at a rate of about 200 cal/d or the caloric equivalent of one spawning batch would be stored about every 5 d.

TABLE 5.—Maximum and minimum fat content of female northern anchovy from Southern California Bight in 1965-67.[1]

	Fat content (% dry weight)				Period of maximum rate of increase in fat stores	
	Minimum		Maximum			
Year	Mo.	%	Mo.	%	Mo.	Total days
1965	Apr.	13.0	Nov.	39.8	June-Aug.	59
1966	Mar.	15.0	July	40.0	May-June	60
1967	Apr.	18.2	June	43.5	Mar.-May	69
Mean		15.4		41.1		63

[1]Data illustrated in Figure 8; from Lasker and Smith (1977).

This analysis indicates that the annual spring bloom might regulate the reproductive potential of the northern anchovy population. This effect may have a 1-yr lag because fat accumulated in the late spring and summer would presumably be used to support reproduction the following year because most spawning occurs in February through April. On the other hand, if 20 spawnings occur, about one-third of them would have to be supported from energy gained during the current year. Thus, production of plankton might have an effect on egg production late in the spawning season, but the major effect of the spring bloom on reproduction may occur the following year.

ENERGY BUDGET FOR FEMALE GROWTH AND REPRODUCTION

In this section we calculate an annual energy budget for reproduction and growth in female northern anchovy based on relationships established in past sections and in the laboratory ration study outlined below. Food ration (R) may be partitioned into energy losses of metabolism (Q), excretion (X), digestive losses (I), reproductive costs (S), gains in growth (N) and fat stores (F) where

$$R = Q + X + I + S + N + F. \quad (7)$$

We do not estimate Q, X, or I, but rather calculate for laboratory females the gross conversion efficiency (C) where

$$C = \frac{S + N + F}{R}. \quad (8)$$

Variables N and F were calculated by subtracting weight and fat content of females determined at the beginning of the experiment from that determined at the end (Table 6); reproductive cost S was simply the increase in weight of the ovary since the fish did not spawn during the experiment; and R was calculated using Equation (5).

The coefficient C was used to estimate ration for natural populations using

$$R = \frac{S + N}{C}. \quad (9)$$

TABLE 6.—Calories gained per day and daily ration of two groups of northern anchovy fed Oregon Moist Trout Pellets.

Item	Standard length (mm)		Fat-free dry weight (without ovary) (g)		Fat in body (without ovary) (g)		Ovary dry weight (including fat) (g)	
	Beginning	End	Beginning	End	Beginning	End	Beginning	End
			Group 2					
Mean	108	120	2.38	3.27	1.17	2.66	0.14	0.38
SE of mean	.86	1.04	.09	.12	.30	.18	.02	.02
Number of fish	21	19	21	19	21	19	21	21
			Group 3					
Mean	106	122	2.16	3.30	.70	2.54	.04	.38
SE of mean	1.51	1.31	.10	.08	.03	.11	.02	.03
Number of fish	24	18	24	18	24	18	24	18

Group	Duration of experiment (d)	Daily ration[2] (cal)	Calories gained per day[1] Body (less ovary) (fat free)	Fat	Ovary (including fat)	Total
2	69	2,238	53	199	19.8	271
3	78	2,245	60	218	24.9	303
Mean	73.5	2,241	56	208	22.4	287
Percentage of ration			2.5	9.2	1.0	12.8

[1] Caloric values in Table 2.
[2] Method of calculation of ration outlined in methods.

Fat stores (F) are included in calculation of C in the laboratory work (Equation (8)) but not in the ration for natural populations (Equation (9)) because on an annual basis it is assumed to be subsumed in the annual cost of reproduction. The caloric value used for growth was set at the minimum fat content of the year (15.4% of the dry weight) using values in Table 2 and Equation (1).

Laboratory Growth Efficiency

Northern anchovy (groups 2 and 3) maintained in the laboratory grew much faster than those in the sea. The growth in length was about four times that estimated for wild northern anchovy by Spratt (1975) but was seven times faster when Spratt's data were converted to wet weight using the length-weight conversion for females of Collins (1969) (solid line, Figure 9). Thus, the average ration consumed by northern anchovy in the laboratory, 2,241 cal/d (about 124 cal/g fish wet weight per d) is probably much larger than the one consumed in the sea. On a wet weight basis, the laboratory ration (4.5% of fish wet weight/d) is deceptively low because the pelleted food had a much lower water content (35%) than natural foods (85%). A caloric equivalent ration of natural foods (copepods) would be about 16% of the wet weight/d.

Spawning did not begin during the experiment, hence the proportion of the daily ration incorporated into the ovaries (0.8%) was a function of only maturation of the ovary (Table 6). The median of the mean major axis of the eggs in the most advanced batch in the ovary increased from 0.55 to 0.63 mm in group 2 and from <0.25 to 0.63 mm for group 3. Most of the caloric gain was in fat; the percentage of the dry weight that contained fat increased from 32.6 to 44.2% in group 2 and from 24.5 to 43.2% in group 3 and accounted for about 9.2% of the daily ration. The caloric conversion efficiency for the total gain of calories in the body (including ovary and fat) was 12.8%. We calculated from data of Takahashi and Hatanaka (1960)

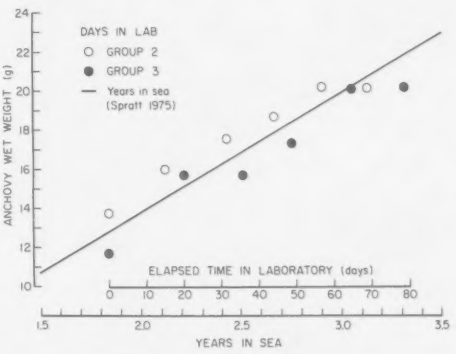

FIGURE 9.—Growth in days of two groups of northern anchovy in the laboratory (dots and circles) compared with the growth over years of northern anchovy in the sea (solid line). Growth in the laboratory is plotted using upper scale (elapsed time days), and growth in sea (solid line, from Spratt 1975; Collins 1969) is plotted on lower scale (years); and ratio between scales is about 1:7. Each point is mean weight for 8-12 fish. Laboratory fish were fed a pelleted trout ration which was the caloric equivalent in natural foods of about 16% of the fish wet weight per day.

that the Japanese anchovy, *Engraulis japonicus*, fed *Euphausia pacifica* in the laboratory, had a gross growth efficiency (in calories) of 11.9%, which is similar to our estimate of 12.8% for *E. mordax*.

Energy Budget

Growth of northern anchovy in the sea from age 1 to 2 yr is equivalent to a gain of 6.2×10^3 cal, and the energy cost of 20 spawnings for a 1-yr-old female is about 10×10^3 cal (documentation given in Table 7). Assuming that the caloric conversion efficiency for northern anchovy in the sea is the same as in the laboratory (12.8%), 1-yr-old females (mean weight 10.3 g) consume annually about 127×10^3 cal of which 8% would be used for reproduction and 5% for growth. This implies a daily rate of consumption in the sea of 348 cal/d, or, on a wet weight basis, about 4% body wet weight/d in copepods (copepods = 5,252 cal/g dry weight, Laurence (1976); water content of *Calanus* = 84.7%, Lovegrove (1966)). Sirotenko and Danilevskiy (1977) estimated from stomach content analysis that the Black Sea anchovy, *E. encrasicholus*, consumed 1.5-3.7% of their body weight/d; Mikhman and Tomanovich (1977) estimated from field captured specimens that *E. encrasicholus* consumed 1.4-3.0% of their body weight/d when they fed upon phytoplankton, 3.4% when they ate zooplankton, and 9.3% when they ate benthic animals. Our estimate of 4-5% body weight/d for females 1-3 yr old is within the range of these values.

DISCUSSION

Spawning Frequency

Northern anchovy females matured eggs in the laboratory at the rate required for weekly spawning, thus supporting the conclusions of Hunter and Goldberg (1980) and Hunter and Macewicz (1980). Our estimates of reproductive effort (egg calories/ration calories) of 8-11% (Table 7) seem reasonable, thereby supporting our estimate of 20 spawnings/female per year. Our calculations indicate that this effort could be sustained by a daily ration of natural foods of 4-5% of the fish wet weight/d which is similar to the natural ration of *E. encrasicholus* (Sirotenko and Danilevskiy 1977; Mikhman and Tomanovich 1977). Few estimates of reproductive effort exist for fishes. Lasker (1970) estimated that the cost of reproduction in Pacific sardine, *Sardinops sagax*, was about 1% of the total annual caloric requirement. He assumed the caloric equivalent of the ovary is spawned per year, which now seems an underestimate. Constantz (1976) estimated that reproductive effort ranged from 4 to 15% in two populations of *Poeciliopsis occidentalis*. Hirshfield (1977) found in laboratory studies that reproductive effort was related in a complex fashion to temperature and ration in medaka, *Oryzias latipes*; he estimated reproductive effort ranged from 10 to 18% in two natural Japanese populations. We conclude that 20 spawnings/yr is a reasonable estimate of the number of spawnings produced by females in the northern anchovy central subpopulation. The fact that two-thirds of the cost could be supported by the average annual decline in fat stores supports this conclusion.

An implication of this study is that egg maturation and vitellogenesis are continuous during peak spawning months. Evidence for this includes: the large fraction of the females in the population spawning per day during peak spawning months (10-16%); the presence of the caloric equivalent of only one or two spawning batches in the ovary at any time; the inverse relation between the abundance of egg sizes in the ovary and oocyte maturation rate; and the continuation of egg maturation until the last batch of eggs is spawned. Although maturation and vitellogenesis probably continue for extended periods, the rates probably vary. The seasonal decline in the fraction of females in the

TABLE 7.—Annual energy budget for female northern anchovy.

Age (yr) Beginning-end	SL[1] (mm) Beginning-end	Wet weight[2] (g) Beginning-end	Annual energy budget (thousands of calories)			Percentage of ration	
			Growth[3]	Reproduction[4]	Ration[5]	Growth	Reproduction
1-2	93-112	7.33-13.25	6.24	10.00	127	5	8
2-3	112-126	13.25-19.33	6.38	21.0	214	3	10
3-4	126-136	19.33-24.69	5.60	34.3	312	2	11

[1]From Spratt (1975).
[2]From Equations (1) and (2) where 15.4% of dry weight = fat.
[3]Gain in calories assuming 15.4% of dry weight = fat; caloric values in Table 2.
[4]Caloric content of 20 spawning batches; batch size calculated for mean female wet weight over the year (method illustrated in Table 4).
[5]Reproduction calories + growth calories/0.128, where 0.128 is growth conversion efficiency determined in laboratory (Table 6).

population spawning per day indicates that either the interval between spawnings in individual females increases in the latter part of the spawning season, or that an increasing number of females cease spawning as the season progresses, or a combination of both events. Rates of egg maturation and vitellogenesis probably also vary within a single maturation-spawning cycle. The caloric content of a northern anchovy ovary about doubles over the interval between spawnings (7-10 d in peak spawning months), indicating a rapid rate of vitellogenesis after spawning. In *Brachydanio rerio*, which spawns at 5-d intervals, a marked increase in gonadotropic activity occurs in the pituitary immediately after spawning (Lambert and van Oordt 1974), followed 1-2 d later by histological signs of an increase in lipoprotein production in the liver correlated with an increase in vitellogenesis (Peute et al. 1978). Similar processes may occur in northern anchovy, causing cyclic changes in the rates of vitellogenesis and egg maturation within the interval between spawnings.

Our estimate of 20 spawnings/yr is much higher than the number of spawnings estimated for many other pelagic spawning clupeoid fishes or for pelagic spawners in general. Multiple spawning fishes such as pilchards, sardines, anchovies, jack mackerels, and mackerels are often believed to produce one to three and possibly more spawning batches per year. These conclusions are based on the fact that frequently two modes of yolked eggs and sometimes three (in females with hydrated eggs) are observed in frequency distributions of ovarian egg sizes. Eggs are distributed in the same way in the northern anchovy (MacGregor 1968; Hunter and Goldberg 1980), but as present studies indicate, estimates of one to three spawnings would be in error by a factor of about 10. Thus, comparisons of annual fecundity among pelagic spawning clupeoids are meaningless at present, and spawning biomass estimated from egg and larval surveys may be in error because the total fecundity is inaccurate. Because of this it is essential that spawning frequency be estimated for additional species.

The best approach, at present, is the histological technique of Hunter and Goldberg (1980), but counts of the number of females with hydrated eggs could be used if histological techniques are impractical. Females with hydrated eggs are often rare in collections of clupeoid females taken during the spawning season (Higham and Nicholson 1964; Leary et al. 1975). Females with hydrated eggs may be available for sampling for only a short period of each day because hydration is rapid and spawning soon follows hydration. In northern anchovy, hydration is completed in about 12 h, but the earliest stage may not be evident without histological examination. In tropical species the time available for sampling females with hydrated eggs may be even less because of elevated temperature. The daily pattern of hydration and spawning must be known to use hydrated eggs as a measure of spawning frequency. It may also require sampling of fish in the day, because many pelagic spawners such as the northern anchovy begin spawning at sunset (Blaxter and Holliday 1963; Leary et al. 1975; Hunter and Macewicz 1980).

Variation in Egg Production and Reproductive Effort

Annual egg production and/or reproductive effort in northern anchovy populations can be modulated by changes in batch fecundity, annual number of spawnings, female size at first maturity, egg size, and egg cannibalism. Some evidence exists for each of these mechanisms in northern anchovy populations; we consider the evidence below.

Batch fecundity was relatively constant over 1978-79 (Hunter and Macewicz 1980) and was similar to that of laboratory specimens fed a large food ration. On the other hand, MacGregor (1968) estimated a somewhat higher fecundity for the central stock in the 1950's than Hunter and Macewicz (1980) did for the 1970's, and Laroche and Richardson (1981) found that batch fecundity of the northern subpopulation (Oregon coast) was much higher than all estimates for the central stock. Batch fecundity certainly differs between central and northern subpopulations, and it seems possible that it may have varied within the central stock over the last decades. Nevertheless, batch fecundity within a subpopulation may be a relatively more stable reproductive characteristic than other reproductive traits.

Weight at first maturity and age structure of the spawning population have a major effect on egg production, since batch size in northern anchovy increases exponentially with weight. Clark and Phillips (1952) concluded for females taken in 1946-52 from the central subpopulation that 50% of northern anchovy reach maturity at 130 mm SL

whereas Hunter and Macewicz (1980) estimated for 1979 that 50% of females of 96 mm SL were mature. Laroche and Richardson (1981) reported that only 31% of females 85-100 mm SL from the northern stock were mature. Thus, size at sexual maturity varies between subpopulations and may have varied within the central subpopulation over the last decade.

The relatively short 2-mo spawning season of the northern subpopulation of northern anchovy (perhaps 4 to 8 spawnings, Hunter and Macewicz 1980) compared with the central subpopulation (20 spawnings) is evidence of the great plasticity in the annual number of spawnings. Plasticity in the number of spawnings of the central stock is also indicated by the dynamics of the central population over the last decades. Smith (1972) pointed out that the decline of the Pacific sardine population was accompanied by an increase in the duration of the northern anchovy spawning period. Before the Pacific sardine decline, most northern anchovy spawning occurred in the winter quarter, whereas now larval production in both quarters is about equal. This increase in the duration of the peak period of spawning indicates that the annual number of spawning batches produced by northern anchovy has changed significantly since the demise of the Pacific sardine population. Food made available by the collapse of the Pacific sardine population may have been used by the northern anchovy population to increase the number of spawning batches produced annually. The fact that these additional spawnings occurred during the period Pacific sardine normally spawned may have had an important effect on the Pacific sardine population.

The annual seasonal decline in egg size in northern anchovy population (central stock) resembles that reported for other clupeoid fishes (Blaxter 1969; Ciechomski 1973; Le Clus 1979). Production of smaller eggs late in the season may be an energy-sparing mechanism whereby fecundity is maintained constant but at a lower reproductive effort. This could represent a 20% savings in reproductive costs in northern anchovy. Bagenal (1973) concluded in his review of the literature that it seems likely a negative correlation exists between fecundity and egg size. Several other mechanisms are possible; egg size may increase with female age (Hirshfield 1977), and the seasonal change could be caused by seasonal changes in the age structure of the spawners. In this case smaller eggs may compensate for the energy cost of faster growth in young fish. Alternatively, egg size may decline in females as ration increases during the spring and summer. Bagenal (1969) found that higher ration in brown trout resulted in more and smaller eggs. On the other hand, Hislop et al. (1978) found that the dry weight of eggs produced by haddock in the laboratory declined with successive spawnings and that the dry weight of eggs tended to be lower in females fed a lower ration. In northern anchovy, there may be a change in the partitioning of energy between growth and reproduction during late spring and summer when the potential for growth is higher, and this could result in the production of smaller eggs. As egg size alters the survival potential of the larva (Blaxter and Hempel 1963), any of these mechanisms could have important consequences because it could alter the relative contribution to recruitment of spawn produced in the latter part of the spawning season.

Egg cannibalism may also be an important factor regulating the effective egg production, as intensity of cannibalism could change with population size. Hunter and Kimbrell (1981) concluded that ingestion of eggs by northern anchovy could account for 17% of the daily egg production during peak spawning months.

This discussion indicates that egg production and reproductive effort of northern anchovy populations probably changes in a complex manner in relation to food, growth, temperature, population size, and age structure. All the reproductive parameters we have discussed may vary to some degree over years, between subpopulations, or within a season.

Studies of the reproductive energetics of northern anchovy populations will eventually require consideration of males as well as females. We know little about males at present. Our laboratory data indicated that males consume slightly less food than females, but no difference existed when consumption was expressed on a unit weight basis. Growth curves for male and female northern anchovy (Collins 1969) indicate that females are slightly longer than males of the same age, but the difference is small (about a 2% difference in length) and probably not statistically significant. Other than this small difference in size, no obvious sexual dimorphic characters exist. Schools have highly biased sex ratios (Klingbeil 1978), and males predominate in actively spawning schools (Hunter and Goldberg 1980). This suggests that

males may remain reproductively active for longer periods within the spawning season and may not have as well defined spawning cycles as do females. These differences are small relative to the overall great similarity between the sexes.

ACKNOWLEDGMENTS

Gary Stauffer (SWFC), who developed one of the original versions of the ration equation, provided guidance in its application in the present study. Carol Kimbrell (SWFC) carried out much of the statistical analysis, collected some of the data, and provided editorial assistance. The estimates of spawning frequency are based primarily on the careful histological analysis of Beverly Macewicz (University of California, San Diego), and Thomas Mickel (University of California, Santa Barbara) assisted in laboratory work.

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DEVELOPMENT OF LARVAE AND JUVENILES OF THE ROCKFISHES *SEBASTES ENTOMELAS* AND *S. ZACENTRUS* (FAMILY SCORPAENIDAE) AND OCCURRENCE OFF OREGON, WITH NOTES ON HEAD SPINES OF *S. MYSTINUS*, *S. FLAVIDUS*, AND *S. MELANOPS*[1]

WAYNE A. LAROCHE AND SALLY L. RICHARDSON[2]

ABSTRACT

Developmental series of larvae and juveniles of two species of northeast Pacific rockfishes (Scorpaenidae: *Sebastes*) are described and illustrated: *S. entomelas* (9.9-74.5 mm standard length) and *S. zacentrus* (7.4-74.8 mm standard length). Descriptions include literature review, identification criteria, distinguishing features, general development, morphology, fin development, spination, scale formation, and pigmentation.

Ontogeny of *S. entomelas* is very similar to that of *S. flavidus* and *S. melanops* among species for which development is known. All have moderately slender bodies and moderately developed head spines. Pigment patterns develop similarly but pigmentation is less intense in *S. entomelas*. Larval and juvenile *S. entomelas* within the size range described are distinguished by presence of preocular and supraocular spines, pectoral fin rays usually 18, dorsal fin rays usually ≤8, lateral line pores 52-56, and lack of melanophores at the articulation of dorsal and anal fin rays. Ontogeny of *S. zacentrus* is rather distinctive among species for which development is known. Larvae and juveniles are relatively deep bodied with large head spines. They are distinguished by presence of preocular and absence of supraocular spines, pectoral fin rays usually 17, dorsal fin rays usually 14, anal fin rays usually 7, lateral line pores 38-48, gill rakers 32-37, and relative lack of pigment.

Young of *S. entomelas* were taken March-July and *S. zacentrus* August-December off Oregon. Larvae of *S. zacentrus* seemed to have a more restricted offshore distribution than reported for most other species, possibly a function of seasonal wind and current regimes.

Additional new information concerning variation in supraocular spine patterns is presented as supplemental data to aid in identification and separation of four similar species, *S. entomelas*, *S. flavidus*, *S. melanops*, and *S. mystinus*.

The rockfish, *Sebastes* spp., resources of the northeast Pacific Ocean are being subjected to increasing fishing pressure. In 1978, trawl landings of rockfishes (all species) by the United States and Canada were 26,000 metric tons (t) or 38% of total Pacific landings (Pacific Marine Fisheries Commission 1964-78). This represents a sizable increase in the catch of "other rockfish" from previous years, e.g., 20,100 t in 1978 compared with 15,700 t in 1977 and 9,900 t in 1976 (Pacific Marine Fisheries Commission 1964-78). Since many rockfish species are long lived, living over 20 yr (Phillips 1964; Westrheim and Harling 1975), overfishing could have serious consequences. Rational utilization of these important resources requires an understanding of the life history and biology of each species involved. Yet, such information is still lacking for most of the rockfishes.

This paper provides some of the first information on the early life history of *S. entomelas*, widow rockfish, and *S. zacentrus*, sharpchin rockfish. *Sebastes entomelas* was one of five principal species in Oregon bottom trawl landings of "other rockfish," composing 13% of the catch during the years 1963-71, although annual catches fluctuated from 168 to 1,074 t (Niska 1976). Introduction of midwater trawl fishing for rockfish has recently focused attention on *S. entomelas* since large catches have been landed, e.g., during a 4-mo period in 1979 >90% of the 909 t of rockfish landed in Oregon were *S. entomelas* (Barss[3]). *Sebastes*

[1]From a final report for NOAA-NMFS Contract No. 79-ABC-00087 submitted to Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, on 31 July 1979.

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[3]William Barss, Fishery Biologist, Oregon Department of Fish and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. July 1979.

Manuscript accepted December 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

zacentrus was landed in Oregon from 1963 to 1971 but never in large quantities (Niska 1976), possibly due to its reported preference for a rough bottom (Gunderson[4]).

Development of larvae and juveniles of *S. entomelas* and *S. zacentrus* is described and compared with other species of *Sebastes* for which young stages are known. Occurrence of young off Oregon is discussed. Additional new information is presented on head spine patterns and variability among the group of four similar species, *S. entomelas*, *S. flavidus*, *S. melanops*, and *S. mystinus*, which cooccur off Oregon. This information will aid in identification and separation of these species, particularly of specimens with variant head spine patterns.

METHODS

Specimens described in this paper came from collections in the School of Oceanography, Oregon State University. Most collections were obtained with 70 cm bongo nets, neuston nets, meter nets, purse seines, Isaacs-Kidd midwater trawls, beam trawls, otter trawls, and commercial midwater trawls off the Oregon coast since 1961. Samples were taken during all months of the year and along the entire Oregon coast but were concentrated along an east-west transect off Newport, Oreg. (lat. 44°39.1′ N). Benthic juveniles of *S. entomelas* were taken from adjacent California waters (lat. 40°12.2′ N, long. 124°23.4′ W). All specimens were preserved in 5 or 10% Formalin[5] and transferred to 40% isopropyl alcohol.

Our approach to identification, methods of making counts and measurements, and terminology for development and spination follow Richardson and Laroche (1979) and Laroche and Richardson (1980). Body parts measured include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of hindgut at anus.

Head length (HL) = snout tip to cleithrum until no longer visible, then to posteriormost margin of opercle.

Snout length = snout tip to anterior margin of orbit of left eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest diameter of left orbit.

Interorbital distance = distance between dorsal margins of orbits.

Body depth at pectoral fin base = vertical distance from dorsal to ventral body margin at base of pectoral fin.

Body depth at anus = vertical distance from dorsal to ventral body margin immediately posterior to anus.

Caudal peduncle depth = shortest vertical distance between dorsal and ventral margins of caudal peduncle.

Caudal peduncle length = horizontal distance from base of posteriormost dorsal ray to posterior margin of hypural elements.

Pectoral fin length = distance from base to tip of longest ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic spine length = distance from base to tip of pelvic spine.

Pelvic fin length = distance from base to tip of longest ray.

Snout to origin of pelvic fin = distance along body midline to vertical through insertion of pelvic fin.

Parietal spine length = distance along posterior margin of parietal spine from insertion to tip.

Nuchal spine length = distance along posterior margin of nuchal spine from insertion to tip.

Preopercular spine length (third spine; posterior series) = distance from tip to basal insertion if visible, or to a line connecting the points of deepest indentation between preopercular spines 2 and 3 and spines 3 and 4 (posterior series).

Longest dorsal fin spine = distance from base to tip.

Longest dorsal fin ray = distance from base to tip.

Longest anal fin spine = distance from base to tip.

All body lengths given refer to standard length unless noted otherwise. When the two posteriormost dorsal and anal fin rays arise from the same pterygiophore, they are counted as one.

[4]Gunderson, D. 1976. Proceedings of the 1st rockfish survey workshop. Processed rep., 14 p. Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

SEBASTES ENTOMELAS (JORDAN AND GILBERT)

Literature (Figures 1-3).—The pigment pattern of preextrusion *S. entomelas* larvae was described by Harling et al.,[6] including a figure, and Westrheim (1975). Preextrusion larvae, mean 4.8, 5.0 mm TL, have a row of usually <16 melanophores along the ventral body midline which stops short of the anus by at least four myomeres. The gut is pigmented in the vicinity of the anus. Pigment is absent from the dorsum, head, and hypural region. In reared larvae, the number of ventral midline melanophores increases to >16 (Westrheim 1975).

Identification (Tables 1-3; Appendix Table 1).—Fifty-three specimens of *S. entomelas* (9.9-74.5 mm) were selected for the development series from 444 larval and juvenile specimens identified. Juveniles were identified using the following combination of characters observed in juvenile and adult specimens examined:

Gill rakers = 34-39
Lateral line pores = 52-56

[6]Harling, W. R., M. S. Smith, and N. A. Webb. 1971. Preliminary report on maturity, spawning season, and larval identification of rockfishes (*Sebastodes*) collected during 1970. Fish. Res. Board Can., Manuscr. Rep. Ser. 1137, 26 p.

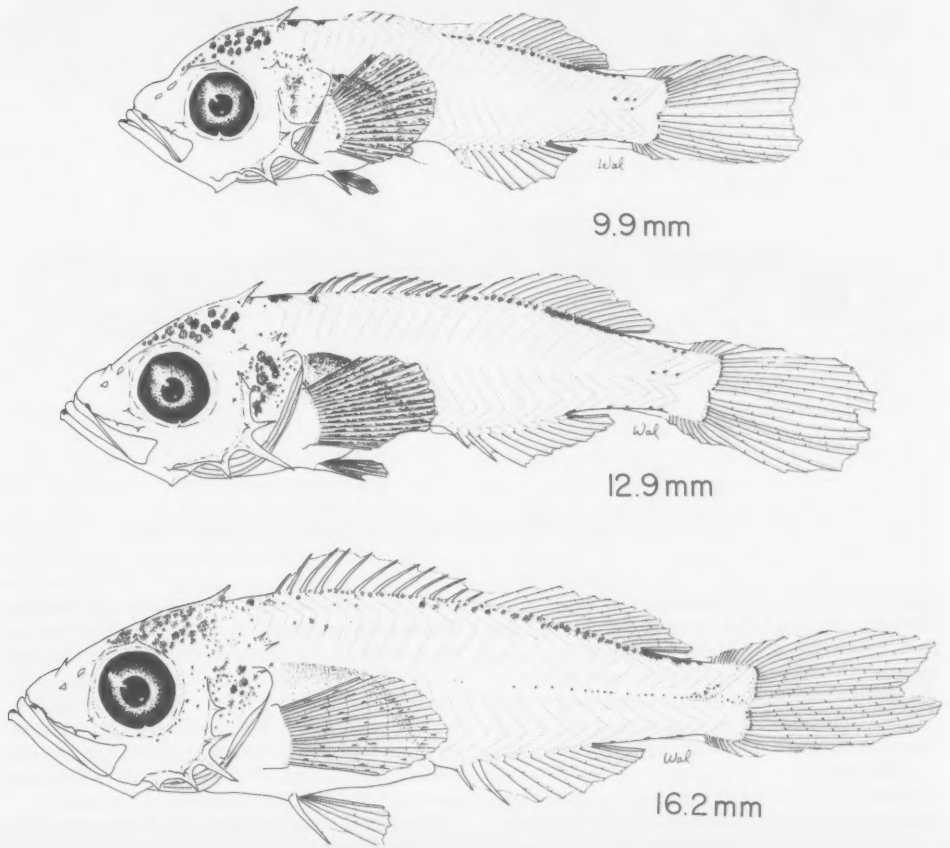

FIGURE 1.—Pelagic larvae of *Sebastes entomelas*.

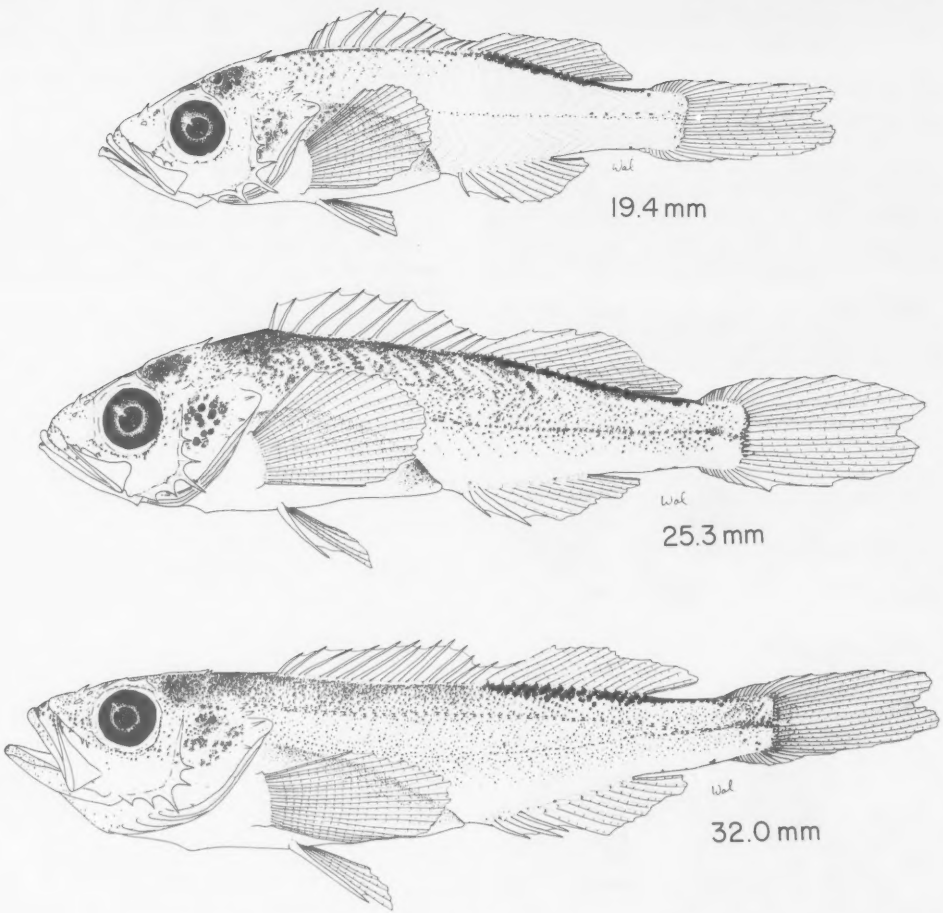

FIGURE 2.—Pelagic larvae (19.4, 25.3 mm) and pelagic juvenile (32.0 mm) of *Sebastes entomelas*.

Pectoral fin rays = 17-19, usually 18
Anal fin soft rays = 7-9, usually 8
Dorsal fin soft rays = 14-16, usually 15
Vertebrae = 26
Preocular spine = present (specimens <343 mm)
Supraocular spine = present (specimens <343 mm)
Interorbital space = flat to convex
Black blotch at base of spinous dorsal fin = present as fringe along distal margin of fin membrane.

Of the 36 *Sebastes* species off Oregon (Richardson and Laroche 1979), *S. entomelas* has the best fit to the above characters. Larvae and juveniles of *S. entomelas* are similar to those of *S. flavidus*, *S. melanops*, and *S. mystinus*. Large larvae and juveniles of *S. flavidus* and *S. melanops* lack preocular and usually lack supraocular spines (Laroche and Richardson 1980) which are present in both *S. entomelas* and *S. mystinus*.

Dorsal and anal fin ray counts separate nearly all specimens of *S. entomelas* and *S. mystinus* based on count frequency statistics given by

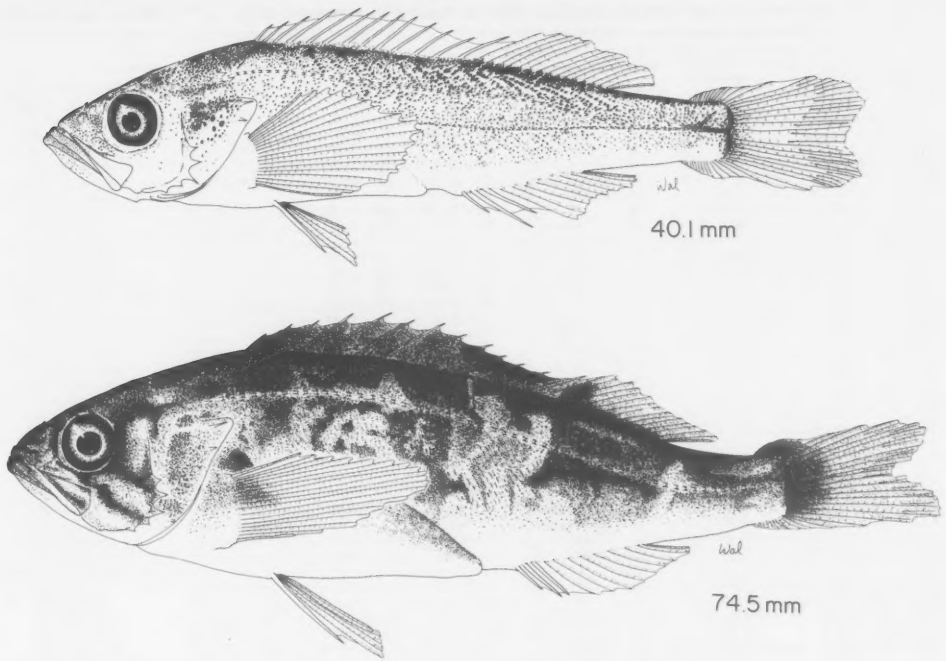

FIGURE 3.—Pelagic juvenile (40.1 mm) and benthic juvenile (74.5 mm) of *Sebastes entomelas*.

Laroche and Richardson (1980). Of 79 *S. entomelas* examined 94% had dorsal fin rays ≤15 and 96% had anal rays ≤8. Of 62 *S. mystinus* examined 92% had dorsal fin rays ≥16 and 90% had ≥ 9 anal fin rays. Only one specimen of *S. entomelas* had >15 dorsal fin rays and >8 anal fin rays. No *S. mystinus* had <16 dorsal fin rays and <9 anal fin rays. In specimens with outlyer dorsal or anal fin ray counts, the numbers of lateral line pores and diagonal scale rows below the lateral line resolved any questions in all cases (see Laroche and Richardson 1980, appendix table 1). To insure that no *S. mystinus* were accidentally included in the developmental series of *S. entomelas*, specimens with either >15 dorsal fin rays or >8 anal fin rays were intentionally excluded.

Pigment pattern and body morphology were also useful in linking smaller specimens to the developmental series.

Distinguishing Features.—Characters useful to distinguish *S. entomelas* larvae (9.9-18 mm) from those of other *Sebastes* species are fin element counts, gill raker counts, moderate pigmentation on pectoral and pelvic fins, presence of pigment along the dorsal body surface beneath the dorsal fin, internal and/or external melanophores above the notochord near the point of flexion, and melanophores along the dorsal and ventral margins of the caudal peduncle. The lack of melanophores at the articulation of anal fin rays helps distinguish *S. entomelas* from *S. flavidus* and *S. melanops* larvae within this size range. The smaller caudal peduncle depth/caudal peduncle length ratio and presence of 18 pectoral fin rays also help to distinguish *S. entomelas* from *S. melanops*. For larvae and juveniles >18 mm, meristic characters, presence of preocular (specimens >22 mm) and supraocular (specimens >18 mm) spines, flat to convex interorbital space, body and fin pigmentation, and body morphometry together serve to distinguish *S. entomelas* from other Oregon species.

General Development.—Notochord flexion is completed by ≈14 mm in *S. entomelas*. Transformation

TABLE 1.—Meristics from larvae and juveniles of *Sebastes entomelas* based on unstained specimens. Counts of left and right pelvic fin rays (I,5; I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7,7) were constant throughout the series. Specimens above dashed line are undergoing notochord flexion.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
9.9	IV+I[1],15	II[1],8	18	18	21+ 8=29	—	—	—	—	—
10.0	([2])	([2])	18	18	20+ 7=27	20+ 6=26	—	—	—	—
10.9	XIII[1],14	III[1],7	18	18	22+ 9=31	22+ 8=30	—	—	—	—
11.0	XIII[1],15	III[1],8	18	18	22+ 8=30	21+ 8=29	—	—	—	—
11.9	XIII[1],15	III[1],8	18	18	22+ 8=30	23+ 8=31	—	—	—	—
12.0	XIII[1],14	III[1],8	18	18	22+ 7=29	22+ 8=30	—	—	—	—
12.9	XIII[1],15	III[1],8	18	18	23+ 8=31	22+ 8=30	—	—	—	—
13.7	XIII[1],15	III[1],8	18	18	24+ 8=32	24+ 8=32	—	—	—	—
14.0	XIII[1],15	III[1],8	18	18	23+ 8=31	23+ 8=31	—	—	—	—
14.9	XIII[1],15	III[1],8	18	18	25+ 9=34	24+ 9=33	—	—	—	—
15.2	XIII[1],15	III[1],8	18	18	24+ 9=33	23+ 9=32	—	—	—	—
16.2	XIII[1],15	III[1],8	18	18	24+10=34	23+ 9=32	—	—	—	—
16.8	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
17.2	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
18.4	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
18.5	XIII[1],15	III[1],8	18	18	24+ 9=33	25+ 9=34	—	—	—	—
19.4	XIII[1],15	III[1],8	18	18	24+10=34	24+10=34	—	—	—	—
20.4	XIII[1],15	III[1],8	18	18	26+10=36	25+10=35	—	—	—	—
20.8	XIII[1],14	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
21.0	XIII[1],15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]21.7	XIII[1],15	III[1],8	18	18	25+ 9=34	24+ 9=33	—	—	—	—
[3]22.3	XIII[1],15	III[1],8	18	18	26+ 9=35	25+ 9=34	—	—	—	—
[3]22.9	XIII[1],15	III[1],8	18	18	25+10=35	26+10=36	—	—	—	—
[3]23.9	XIII[1],15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]24.5	XIII[1],15	III[1],8	18	18	26+10=36	26+ 9=35	—	—	—	—
[3]24.5	XIII[1],15	III[1],8	18	18	25+10=35	25+10=35	—	—	—	—
[3]25.3	XIII[1],15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]25.9	XIII[1],15	III[1],8	18	18	24+ 9=33	25+ 9=34	—	—	—	—
[3]26.5	XIII[1],15	III[1],8	18	18	27+10=37	26+ 9=35	—	—	—	—
[3]26.7	XIII[1],15	III[1],8	18	18	25+10=35	25+ 9=34	—	—	—	—
[3]27.2	XIII,15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]27.9	XIII,15	III[1],8	18	18	26+10=36	25+10=35	—	—	—	—
[3]28.5	XIII,15	III[1],8	18	18	26+10=36	25+10=35	—	—	—	—
[3]29.1	XIII,15	III[1],8	18	18	26+10=36	26+10=36	—	—	—	—
[3]29.7	XIII,15	III[1],8	18	18	25+10=35	26+10=36	—	—	—	—
[3]30.6	XIII,15	III[1],8	18	18	26+ 9=35	25+10=35	—	—	—	—
[4]30.8	XIII,15	III,8	18	18	26+11=37	26+11=37	—	54	—	—
[4]31.6	XIII,15	III,8	18	18	27+10=37	26+10=36	—	53	—	—
[4]32.0	XIII,15	III,8	18	18	26+10=36	26+10=36	—	52	—	—
[4]33.4	XIII,14	III,8	18	18	25+10=35	25+10=35	—	51	—	—
[4]35.7	XIII,15	III,8	18	18	26+10=35	26+10=36	—	53	—	—
[4]36.8	XIII,15	III,8	18	17	24+10=34	26+10=36	—	—	—	—
[4]40.1	XIII,15	III,8	18	18	26+10=36	26+11=37	—	52	—	—
[5]45.0	XIII,14	III,8	18	18	24+11=35	24+11=35	56	54	—	—
[5]47.7	XIII,14	III,7	18	18	27+11=38	28+11=39	52	54	—	—
[5]55.5	XIII,14	III,8	18	18	26+11=37	27+11=38	55	54	—	—
[5]55.7	XIII,15	III,8	18	18	26+11=37	26+10=36	56	55	—	—
[5]64.4	XIII,15	III,8	18	18	26+10=36	26+10=36	53	52	—	—
[5]65.0	XIII,15	III,8	18	18	27+11=38	27+11=38	53	53	64	63
[5]66.1	XIII,15	III,8	18	18	26+11=37	27+10=37	54	56	61	65
[5]71.2	XIII,15	III,8	18	18	26+11=37	26+11=37	54	54	62	66
[5]74.1	XIII,15	III,8	18	18	26+10=36	26+11=37	54	52	66	62
[5]74.5	XIII,15	III,8	19	19	27+11=38	27+10=37	53	56	64	68

[1]Posteriormost dorsal or anal spine appears as a soft ray.
[2]Forming.
[3]Transforming.
[4]Pelagic juvenile.
[5]Benthic juvenile.

from postflexion larvae to pelagic juveniles occurs between ≈22 and 31 mm as indicated by structural change of the dorsal and anal fin "prespines" to sharp, hard spines. Melanistic pigmentation gradually increases over the body through the larval and transformation periods and does not change markedly during transformation. Transition from pelagic to benthic habitat, based on all specimens examined, probably occurs chiefly between 55 and 75 mm. The largest pelagic juvenile was 40.1 mm, and the smallest juvenile taken in a beam trawl was 42 mm long.

Morphology (Tables 2, 3).—Various body parts were measured on 53 selected specimens of *S. entomelas* (9.9-74.5 mm). Relative growth trends are summarized in Table 2.

Perhaps the most distinctive morphometric aspect of larval and small juvenile *S. entomelas* is the relatively slender body. Body depth decreases

TABLE 2.—Body proportions of larvae and juveniles of *Sebastes entomelas* and *S. zacentrus*. Values given are percent of standard length (SL) and head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from number of measurements listed by stage, indicated in footnotes, in Tables 3 and 6.

Item	*Sebastes entomelas*	*Sebastes zacentrus*
Body depth at pectoral fin base/SL:		
Flexion	29.0±0.87(27.9-30.0)	35.2±1.36(33.8-36.5)
Postflexion	27.5±1.56(24.5-29.9)	34.4±1.07(33.1-35.9)
Transforming	25.2±0.80(23.9-26.3)	32.5±1.49(30.4-35.0)
Pelagic juvenile	23.9±0.48(23.1-24.4)	30.0±1.02(27.7-32.0)
Benthic juvenile	27.8±2.44(24.1-31.3)	32.0±1.08(31.1-33.8)
Body depth at anus/SL:		
Flexion	22.3±1.01(20.9-23.9)	24.7±1.53(23.0-25.9)
Postflexion	22.4±1.48(20.2-24.8)	25.8±1.33(23.3-27.4)
Transforming	20.6±0.56(19.3-21.8)	26.1±1.07(25.0-28.4)
Pelagic juvenile	19.7±0.55(18.6-20.2)	24.3±0.82(22.8-25.8)
Benthic juvenile	23.1±1.31(21.1-24.6)	25.8±1.04(24.3-26.7)
Snout to anus length/SL:		
Flexion	56.5±2.09(53.0-58.8)	52.5±1.78(50.6-54.1)
Postflexion	58.5±2.10(54.8-61.2)	57.0±2.34(53.8-62.4)
Transforming	59.4±1.72(55.3-62.3)	60.4±1.84(57.0-62.4)
Pelagic juvenile	61.0±1.24(59.8-62.7)	60.9±1.76(57.4-64.1)
Benthic juvenile	61.5±2.18(59.4-65.1)	58.7±1.62(56.9-61.3)
Snout to pelvic fin origin/SL:		
Flexion	39.4±1.55(37.0-41.2)	38.7±0.61(38.0-39.2)
Postflexion	37.7±2.12(35.1-40.9)	40.6±1.48(37.8-42.4)
Transforming	36.8±1.49(33.3-39.5)	40.8±1.85(38.1-44.8)
Pelagic juvenile	36.3±3.19(33.2-41.9)	39.4±1.43(36.2-42.3)
Benthic juvenile	37.0±1.83(34.8-40.3)	40.9±1.01(40.2-42.5)
Head length/SL:		
Flexion	39.7±2.09(37.2-43.1)	41.9±2.75(39.2-44.7)
Postflexion	36.3±1.82(34.1-39.4)	42.6±2.08(40.2-45.6)
Transforming	35.0±1.75(32.4-38.4)	40.4±1.53(37.6-43.1)
Pelagic juvenile	32.5±1.40(31.2-35.0)	37.5±1.70(34.4-40.4)
Benthic juvenile	32.2±1.90(29.5-35.6)	36.9±0.98(35.8-37.7)
Eye diameter/HL:		
Flexion	31.2±1.90(28.0-33.3)	33.1±2.08(31.6-35.5)
Postflexion	30.1±1.38(28.4-32.7)	32.0±2.13(28.3-34.8)
Transforming	26.8±1.28(25.0-29.1)	29.4±1.74(26.2-32.4)
Pelagic juvenile	26.7±0.92(25.2-28.2)	29.1±1.40(26.7-32.6)
Benthic juvenile	25.8±0.92(24.3-27.3)	31.1±1.96(29.1-33.2)
Upper jaw length/HL:		
Flexion	35.3±4.30(31.2-41.0)	45.9±1.27(45.2-47.4)
Postflexion	41.5±2.61(38.4-45.9)	43.7±2.31(38.6-45.7)
Transforming	39.5±1.90(36.5-43.1)	41.3±2.68(36.4-46.3)
Pelagic juvenile	42.1±1.59(40.2-43.8)	41.0±2.54(35.6-45.3)
Benthic juvenile	39.2±2.57(35.7-43.2)	42.2±2.48(39.7-46.1)
Snout length/HL:		
Flexion	28.3±3.27(22.6-32.0)	26.2±3.27(23.2-29.7)
Postflexion	27.4±1.79(23.9-29.6)	27.9±1.23(26.2-29.6)
Transforming	27.7±1.77(24.4-31.7)	26.4±1.72(24.2-28.8)
Pelagic juvenile	27.2±1.53(26.1-29.8)	26.2±2.12(22.0-31.4)
Benthic juvenile	25.4±2.68(21.1-28.2)	21.8±3.13(18.4-25.2)
Interorbital distance/HL:		
Flexion	30.9±2.04(28.0-33.3)	29.4±2.00(27.7-31.6)
Postflexion	28.8±1.18(25.7-30.1)	28.0±1.76(24.5-31.0)
Transforming	25.1±1.30(23.0-26.7)	25.5±1.85(23.0-29.6)
Pelagic juvenile	23.4±0.79(22.7-24.7)	21.5±1.48(19.1-23.8)
Benthic juvenile	22.6±1.22(20.6-25.0)	16.6±0.81(16.2-17.7)
Angle gill raker length/HL:		
Flexion	10.5±1.52(9.0-12.8)	9.4±1.48(8.4-10.5)
Postflexion	13.4±0.92(11.9-15.1)	13.3±1.16(10.9-14.8)
Transforming	13.2±0.94(11.7-14.7)	15.1±0.95(13.5-16.9)
Pelagic juvenile	14.4±0.75(13.1-15.5)	15.6±1.07(13.3-17.5)
Benthic juvenile	15.9±1.53(13.5-18.0)	16.0±0.32(15.6-16.4)
Longest dorsal spine length/HL:		
Flexion	12.2±3.00(7.7-15.8)	12.4±5.58(6.1-16.8)
Postflexion	24.8±5.64(17.4-32.4)	25.6±3.83(20.9-31.5)
Transforming	28.5±2.64(25.0-31.0)	36.6±3.21(28.8-39.4)
Pelagic juvenile	34.8±2.09(32.8-36.8)	38.0±2.57(33.9-42.9)
Benthic juvenile	32.9±2.20(30.0-36.5)	37.7±2.54(34.2-40.2)
Longest dorsal ray length/HL:		
Flexion	25.5±7.58(10.8-35.7)	24.9±6.54(20.0-32.3)
Postflexion	33.6±4.45(25.5-42.5)	31.1±3.40(27.3-37.0)
Transforming	35.8±2.93(29.8-39.6)	38.4±3.22(33.9-42.9)
Pelagic juvenile	39.8±2.26(36.4-43.3)	40.8±2.56(37.0-45.2)
Benthic juvenile	39.2±2.46(35.7-42.8)	44.6±2.38(40.9-47.0)
Longest anal spine length/HL:		
Flexion	10.2±2.25(7.4-12.9)	13.6±0.92(12.9-14.2)
Postflexion	21.4±4.76(13.8-26.8)	22.4±4.79(16.7-31.5)
Transforming	25.5±3.52(18.8-31.4)	35.3±3.44(30.5-41.6)
Pelagic juvenile	31.9±1.25(30.8-34.2)	41.1±1.96(37.9-44.8)
Benthic juvenile	35.1±3.73(28.2-39.7)	50.7±4.29(46.1-54.9)
Pectoral fin length/SL:		
Flexion	17.1±1.34(15.0-18.6)	15.3±2.30(13.0-17.6)
Postflexion	21.9±1.45(19.3-24.0)	21.5±1.18(20.2-23.6)
Transforming	23.1±1.11(21.5-25.3)	25.2±1.88(21.4-28.1)
Pelagic juvenile	24.2±0.33(23.7-24.6)	26.7±1.27(24.9-29.0)
Benthic juvenile	25.6±1.23(23.4-26.8)	26.4±0.68(25.4-26.9)
Pectoral fin base depth/SL:		
Flexion	10.0±0.77(9.2-11.0)	13.0±1.07(11.8-13.9)
Postflexion	8.8±0.58(8.2-10.2)	10.6±0.69(9.8-12.0)
Transforming	8.0±0.22(7.6-8.4)	9.3±0.39(8.7-10.0)
Pelagic juvenile	7.6±0.16(7.3-7.8)	8.8±0.44(7.9-9.8)
Benthic juvenile	8.4±0.63(7.3-9.1)	9.8±0.25(9.6-10.2)
Pelvic fin length/SL:		
Flexion	10.3±1.34(8.6-11.8)	13.7±1.68(11.9-15.2)
Postflexion	13.8±1.19(11.4-15.7)	17.5±1.75(15.2-21.0)
Transforming	14.5±0.89(12.7-16.0)	20.1±1.27(17.9-21.7)
Pelagic juvenile	16.1±0.34(15.7-16.6)	19.5±0.93(17.3-21.0)
Benthic juvenile	17.5±1.03(16.4-20.0)	21.3±1.04(20.3-22.6)
Pelvic spine length/SL:		
Flexion	6.0±1.82(3.7-8.4)	9.0±3.46(6.5-11.4)
Postflexion	12.0±1.30(10.0-13.6)	15.9±1.80(13.9-19.4)
Transforming	12.2±1.60(9.9-14.4)	19.7±0.80(18.4-20.7)
Pelagic juvenile	13.7±0.51(13.0-14.6)	17.7±1.52(15.3-20.0)
Benthic juvenile	12.7±0.56(11.7-13.4)	15.5±0.92(14.7-16.9)
Parietal spine length/HL:		
Flexion	10.2±1.80(8.4-13.3)	22.6±5.12(16.8-26.5)
Postflexion	8.7±2.56(6.4-11.6)	14.3±2.24(11.9-17.3)
Transforming	3.8±1.30(2.8-5.6)	10.4±1.83(7.7-14.1)
Pelagic juvenile	—	6.9±2.42(3.8-10.7)
Benthic juvenile	0.9±0.47(0.35-1.9)	2.6±0.98(1.6-4.0)
Nuchal spine length/HL:		
Flexion	1.4±1.70(0.0-4.4)	1.5±1.61(0.0-3.2)
Postflexion	3.4±0.65(2.2-4.1)	5.1±1.36(2.3-7.4)
Transforming	2.0±0.47(1.4-3.0)	4.6±1.74(0.0-6.2)
Pelagic juvenile	1.7±0.33(1.5-2.1)	3.3±1.30(1.2-5.6)
Benthic juvenile	0.0±0.00(0.0-0.0)	0.0±0.00(0.0-0.0)
Procpercular spine length/HL:		
Flexion	20.3±0.69(19.6-21.3)	32.9±8.20(27.1-38.7)
Postflexion	20.1±2.79(15.5-24.1)	25.3±2.35(22.2-29.5)
Transforming	10.8±1.31(8.8-12.3)	22.3±2.96(16.0-25.9)
Pelagic juvenile	5.3±1.60(3.8-7.0)	12.7±4.37(6.7-19.5)
Benthic juvenile	4.2±0.95(3.4-6.5)	4.0±0.87(3.1-5.1)
Caudal peduncle depth/SL:		
Flexion	12.4±0.83(10.9-13.6)	11.8±1.06(10.8-12.9)
Postflexion	11.1±0.71(10.1-12.4)	11.0±0.50(9.9-11.6)
Transforming	9.6±0.37(8.9-10.1)	10.6±0.49(9.8-11.5)
Pelagic juvenile	8.7±0.53(7.8-9.2)	9.6±0.41(8.6-10.3)
Benthic juvenile	9.1±0.34(8.8-9.9)	9.3±0.24(9.0-9.6)
Caudal peduncle length/SL:		
Flexion	15.6±0.78(14.5-16.7)	16.0±0.62(15.3-16.5)
Postflexion	15.3±0.58(14.3-16.2)	14.5±0.86(12.9-15.2)
Transforming	15.4±0.70(14.1-16.7)	14.7±0.68(14.0-15.7)
Pelagic juvenile	15.5±0.98(14.2-16.6)	14.0±0.99(12.4-16.5)
Benthic juvenile	14.6±0.68(13.7-15.7)	13.9±0.33(13.5-14.4)
Caudal peduncle depth/caudal peduncle length:		
Flexion	0.80±0.085(0.70-0.94)	0.74±0.095(0.67-0.85)
Postflexion	0.73±0.051(0.67-0.81)	0.76±0.061(0.67-0.88)
Transforming	0.63±0.030(0.58-0.67)	0.72±0.040(0.68-0.83)
Pelagic juvenile	0.57±0.055(0.47-0.63)	0.69±0.048(0.59-0.79)
Benthic juvenile	0.63±0.028(0.58-0.66)	0.67±0.022(0.65-0.70)

TABLE 3.—Measurements (millimeters) of larvae and juveniles of *Sebastes entomelas*. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal-hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
9.9	12.5	5.4	3.9	1.0	—	1.2	1.2	2.8	2.1	1.2	1.6	1.8	1.0	0.50	0.90	3.8	0.52	0.04	—	0.36	0.30	0.92	0.24
10.0	12.5	5.3	3.9	0.88	1.6	1.3	1.3	3.0	2.2	1.2	—	1.5	1.1	0.39	0.86	3.7	0.36	[4]	0.80	0.36	—	0.42	—
10.9	13.7	6.3	4.7	1.3	1.9	1.5	1.4	3.2	2.6	1.4	1.7	1.8	1.0	0.98	1.2	4.4	0.45	0.04	1.0	0.47	0.58	1.4	0.50
11.0	14.0	6.4	4.2	1.3	1.4	1.4	1.4	3.3	2.5	1.5	1.6	1.8	1.2	0.72	1.0	4.2	0.48	0.10	0.84	0.38	0.50	1.5	0.32
11.9	15.2	7.0	5.0	1.6	1.7	1.4	1.4	3.5	2.7	1.5	1.8	2.2	1.2	1.0	1.4	4.9	0.42	0.22	0.98	0.60	0.76	1.3	0.54
12.0	15.3	6.8	4.7	1.4	1.5	1.4	1.5	3.4	2.7	1.5	2.0	2.0	1.1	0.76	1.4	4.9	0.44	[4]	0.92	0.60	0.50	1.2	0.56
12.9	16.2	7.3	4.8	1.4	1.5	1.5	1.4	3.6	2.7	1.4	2.0	2.4	1.2	1.0	1.4	5.1	—	—	1.0	0.54	0.76	1.3	0.62
13.7	17.5	8.1	5.4	1.4	2.1	1.6	1.6	4.1	3.4	1.7	2.1	2.9	1.4	1.4	1.8	5.6	0.66	0.22	1.3	0.64	0.94	1.5	0.81
14.0	17.3	8.5	5.5	1.6	2.2	1.7	1.5	3.9	2.9	1.6	2.0	2.7	1.2	1.4	1.6	5.7	0.62	0.22	1.2	0.75	—	1.4	0.76
14.9	19.2	9.1	5.4	1.6	2.3	1.7	1.6	4.2	3.6	1.8	2.3	3.1	1.3	1.7	1.8	5.7	0.36	0.22	1.1	0.76	1.3	1.8	1.2
15.2	19.0	9.3	5.5	1.6	2.3	1.8	1.6	4.5	3.7	1.8	2.4	3.0	1.4	—	2.0	6.1	0.64	0.12	1.2	0.72	0.96	1.7	0.82
16.2	20.7	9.4	6.1	1.8	2.7	1.9	1.8	4.7	3.8	1.8	2.5	3.4	1.5	—	2.2	6.3	—	0.22	—	0.74	—	1.9	—
16.8	21.0	9.9	6.2	1.7	2.8	1.8	1.8	4.6	3.7	1.9	2.6	3.6	1.5	—	2.3	6.6	—	—	—	0.88	—	—	—
17.2	22.1	10.3	6.1	1.7	2.8	1.9	1.8	4.7	3.9	1.9	2.5	4.0	1.6	2.2	2.6	6.3	0.50	0.22	1.3	0.86	1.7	2.3	1.5
18.4	23.4	10.6	7.0	1.8	2.8	2.0	1.8	5.2	4.2	2.0	2.9	4.2	1.5	2.5	2.7	6.8	0.45	0.18	1.2	0.92	1.8	2.4	1.4
18.5	23.6	10.2	6.3	1.8	2.5	1.8	1.8	4.7	3.9	2.0	3.0	4.2	1.6	2.3	2.5	6.5	0.42	0.24	1.2	0.84	1.8	2.2	1.5
19.4	24.7	10.9	6.7	1.8	2.6	1.9	1.9	5.2	4.2	2.0	3.0	4.4	1.6	2.5	2.7	6.8	—	0.26	—	0.84	—	2.3	1.6
20.4	25.6	12.0	7.3	1.9	2.9	2.2	2.1	5.4	4.3	2.1	3.1	4.9	1.7	—	3.0	7.6	—	0.20	—	0.94	—	2.6	1.8
20.3	26.5	11.4	7.1	1.7	3.1	2.2	2.1	5.1	4.2	2.1	3.0	4.8	1.7	—	3.0	7.3	0.46	0.22	1.1	1.0	2.3	2.5	1.9
21.0	26.4	12.3	7.3	1.9	2.8	2.1	2.2	5.6	4.6	2.2	3.3	4.8	1.8	2.6	3.3	7.6	—	0.22	—	1.1	—	3.1	1.9
[5]21.7	27.0	13.1	8.0	2.2	3.1	2.1	2.1	5.6	4.5	2.2	3.5	4.9	1.8	2.5	3.2	8.4	0.45	0.24	—	1.0	—	2.7	1.5
[5]22.3	—	13.9	8.4	2.2	3.2	2.4	2.1	5.7	4.7	2.2	3.4	4.8	1.8	—	3.3	8.8	0.24	0.16	1.0	1.1	2.1	2.5	1.9
[5]22.9	29.1	13.6	8.1	2.1	3.1	2.2	2.1	6.0	4.8	2.3	3.5	5.2	1.8	2.5	3.1	8.5	0.32	0.22	1.0	0.96	—	2.7	1.9
[5]23.9	30.0	14.3	8.3	2.2	3.5	2.4	2.0	6.0	4.8	2.4	3.7	5.8	1.9	3.2	3.6	8.6	—	0.16	0.90	1.2	2.5	2.9	—
[5]24.5	30.8	14.5	8.7	2.5	3.5	2.2	2.3	6.3	5.1	2.4	4.1	5.7	2.0	2.5	3.5	9.2	—	—	—	1.2	—	3.0	2.0
[5]24.5	30.8	14.5	9.4	2.6	3.7	2.4	2.2	6.4	5.1	2.4	3.7	5.6	1.9	3.0	3.4	9.2	—	0.16	—	1.2	2.7	—	2.6
[5]25.3	32.0	14.9	8.6	2.1	3.2	2.3	2.3	6.4	5.1	2.5	4.1	5.9	2.0	2.5	3.7	9.3	—	—	—	1.2	—	3.4	2.5
[5]25.9	33.9	15.1	9.3	2.8	—	2.4	2.4	6.4	5.3	2.3	4.0	5.9	2.1	—	3.8	9.6	—	—	—	1.3	—	3.1	2.1
[5]26.5	33.2	16.2	8.6	2.4	—	2.5	2.3	6.5	5.4	2.5	4.2	—	2.1	3.2	3.6	10.1	—	—	—	1.2	—	—	—
[5]26.7	33.0	15.1	9.4	2.6	3.8	2.5	2.4	6.5	5.5	2.5	4.1	5.8	2.2	—	3.4	9.8	0.26	0.18	1.1	1.1	2.4	3.2	2.4
[5]27.2	—	16.6	8.8	2.3	3.6	2.4	2.3	6.5	5.4	2.6	4.0	—	2.2	—	3.8	9.6	—	0.20	—	1.1	2.7	3.4	2.4
[5]27.9	33.4	16.7	10.0	2.9	—	2.5	2.3	7.2	5.8	2.8	4.2	6.6	2.2	4.0	4.3	10.4	—	0.14	0.94	1.2	3.1	3.6	2.8
[5]28.5	35.8	16.9	9.6	2.8	3.5	2.5	2.4	7.5	6.2	2.8	4.5	7.2	2.4	—	4.5	10.2	—	—	—	1.3	—	3.8	—
[5]29.1	35.8	16.1	9.7	2.7	3.9	2.7	2.4	7.2	5.9	2.6	4.1	6.5	2.2	3.8	4.1	9.7	—	0.18	—	1.3	—	3.7	—
[5]29.7	—	17.5	10.4	3.3	4.0	2.7	2.5	7.3	6.1	2.8	4.2	6.6	2.3	—	—	10.5	—	0.22	1.1	1.3	—	3.8	2.8
[5]30.6	36.9	18.7	10.2	2.8	4.4	2.8	2.4	7.3	5.9	2.9	4.8	7.6	2.5	4.4	4.9	11.0	—	0.16	0.90	1.5	—	4.0	3.2
[6]30.8	38.5	18.5	9.7	—	—	2.6	2.4	7.4	6.1	2.8	5.1	7.3	2.3	4.2	5.1	11.3	—	0.18	—	1.4	—	4.2	3.0
[6]31.6	39.1	19.8	10.7	2.8	4.3	2.7	2.5	7.3	6.1	2.7	4.5	7.6	2.4	4.6	5.0	11.4	—	0.19	—	1.4	—	3.9	3.3
[6]32.0	39.7	19.4	10.3	2.8	4.2	2.7	2.4	7.6	6.3	2.7	5.1	7.7	2.4	4.4	5.2	10.9	—	0.22	—	1.6	—	4.2	3.2
[6]33.4	41.9	20.9	11.7	—	—	3.3	2.6	8.1	6.2	2.6	5.5	8.2	2.6	4.4	5.5	14.0	—	0.18	—	1.7	3.9	4.6	3.7
[6]35.7	44.0	21.9	11.4	3.4	4.8	3.1	2.7	8.7	7.1	3.3	5.2	—	2.6	4.9	5.6	13.9	—	0.18	0.80	1.6	4.2	—	3.9
[6]36.8	45.7	22.0	11.5	3.0	5.0	3.1	2.7	8.7	7.4	3.3	5.4	9.0	2.8	4.8	5.9	12.2	—	0.24	0.60	1.7	4.2	4.6	3.8
[6]40.1	—	24.0	12.8	3.4	5.6	3.4	2.9	9.8	8.1	3.7	6.4	9.8	3.1	5.5	6.4	13.4	—	0.16	0.48	1.9	4.2	5.0	4.1
[7]45.0	54.2	28.2	15.0	4.2	5.8	4.1	3.3	11.0	9.5	4.2	6.7	11.0	3.3	—	7.6	16.3	0.06	—	0.98	2.2	5.3	5.4	4.6
[7]47.7	58.2	30.9	17.0	4.7	6.5	4.3	3.5	12.4	10.9	4.7	7.1	11.7	3.8	6.1	8.0	18.9	0.06	—	0.84	2.3	5.3	6.5	4.8
[7]55.5	66.7	33.2	17.0	4.8	6.5	4.3	3.8	13.4	12.0	4.9	8.5	13.0	4.3	6.5	9.1	20.2	0.16	—	0.80	2.8	5.5	7.0	5.5
[7]55.7	67.2	34.9	18.5	5.0	6.6	4.6	4.1	14.0	12.0	5.0	8.4	13.7	4.5	6.8	9.3	21.4	0.18	—	0.78	2.5	5.7	6.6	6.8*
[7]64.4	78.9	38.5	19.4	4.1	8.3	5.1	4.6	17.3	15.0	5.7	8.8	16.9	5.7	8.0	11.0	23.6	0.24	—	0.66	3.5	6.4	8.3	7.7*
[7]65.0	79.2	42.3	22.0	5.4	8.3	5.6	5.0	19.7	16.0	6.1	9.6	17.2	5.9	8.5	13.0	26.2	0.16	—	0.80	3.7	6.6	8.1	7.5*
[7]66.1	81.1	39.4	21.7	5.0	8.7	5.8	5.0	19.3	16.2	6.1	10.4	17.7	5.8	8.6	11.9	23.0	0.20	—	0.88	3.4	7.1	8.9	7.7
[7]71.2	86.1	42.3	22.0	5.6	9.5	5.8	5.0	20.5	16.7	6.3	9.9	18.9	6.1	9.6	12.7	25.4	0.24	—	0.80	3.8	7.8	9.1	8.4
[7]74.1	89.1	45.6	23.9	6.6	8.6	5.8	5.1	20.4	17.6	6.6	10.4	19.4	6.6	9.1	12.9	26.2	0.10	—	0.92	3.9	7.5	9.5	8.8
[7]74.5	90.5	44.7	22.0	4.8	9.0	5.8	5.5	21.9	18.2	6.8	10.4	20.0	6.8	9.8	13.1	27.2	0.24	—	0.78	3.8	8.4	9.1	8.9*

[1]Usually fourth or fifth spine.
[2]Usually in anterior one-fourth of fin.
[3]Where indicated by (*) second and third spines equal or the third, otherwise the second measured.
[4]Bump.
[5]Transforming.
[6]Pelagic juvenile.
[7]Benthic juvenile.

from 29 to 24% through the pelagic juvenile period after which it deepens to 28% SL.

Fin Development (Tables 1-3).—The adult complement of 17-19 (usually 18) pectoral fin rays is present in the smallest larva (9.9 mm). Pectoral fin length increases from 17 to 26% SL between flexion and benthic juvenile stages. The smallest larvae (≈10 mm) have the adult pelvic fin complement (I,5). Pelvic fin length is moderate, increasing from 10 to 18% SL between flexion and benthic juvenile stages. Pelvic spine length increases from 6 to 12-14% SL.

The adult complement of 8 + 7 principal caudal fin rays can be counted on the smallest (9.9 mm) flexion larva. Seven benthic juvenile *S. entomelas*,

59-73 mm, had superior and inferior secondary rays: 12/13 (two specimens), 13/13 (three specimens), and 13/14 (two specimens), as determined from radiographs.

Adults' complements of dorsal and anal fin spines and rays can be counted by ≈11 mm, although ray bases can be counted in the smallest specimen. The dorsal and anal fin prespines become spines by ≈27 and 31 mm, respectively.

Spination (Tables 2, 4).—Spines on the left side of the head of the smallest *S. entomelas* include the parietal; nuchal; first and third anterior preopercular spines; first (as a bump), second, third, and fourth posterior preopercular spines; superior opercular spine (as a bump); postocular; first inferior infraorbital spine; first and fourth superior infraorbital spines; pterotic; and the inferior posttemporal spine.

The parietal spine and ridge are finely serrated on all specimens <33 mm long. Parietal spine length decreases with development becoming overgrown in large juveniles and adults. The nuchal spine, always shorter than the parietal, is usually present in larvae and pelagic juveniles. It begins to fuse with the parietal spine at ≈26 mm and is fused and not recognizable in benthic juveniles (≥45.0 mm).

All five spines of the posterior preopercular series are present on larvae by ≈11 mm and persist through adults. The third spine is always longest but decreases from 20% HL in flexion larvae to 4% HL in benthic juveniles. The second, third, and fourth posterior preopercular spines and the anterior edge of the first spine of the anterior preopercular series are weakly serrated in specimens <30 mm long. Serrations persist on the third posterior preopercular spine to ≈33 mm. The second anterior preopercular spine was present on the left side only in one flexion larva (12.0 mm). The first and third anterior preopercular spines are present on all flexion and postflexion larvae, are reduced to blunt bumps in ≈25 mm transforming larvae, and are no longer recognizable by ≈30 mm.

The superior opercular spine appears well developed and sharp tipped between 10 and 14 mm. The inferior opercular spine appears as a blunt bump at 15 mm, and as a sharp spine in specimens >21 mm. The interopercular spine appears as a blunt bump at ≈11 mm, as a small sharp spine by 22 mm, and is usually reduced to a blunt bump in benthic juveniles >44 mm.

The ridge anterior to the postocular spine is finely serrated on specimens <28 mm. The supraocular spine appears as a bump at ≈18 mm and as a sharp spine by ≈19 mm. The preocular spine appears as a blunt bump at ≈22 mm and as a sharp spine in all specimens >31.6 mm. The first inferior infraorbital spine is present in all specimens <55 mm, and is absent in specimens >56 mm. The second inferior infraorbital spine appears between 10 and 12 mm, is present in all specimens to ≈35 mm, appears only as a blunt bump between ≈33 and 55 mm, and is no longer visible in specimens >55 mm. The third inferior infraorbital spine appears at ≈15 mm, is present between 35 and ≈55 mm, and is usually absent in specimens >55 mm. The first superior infraorbital spine is present in all specimens <26 mm, is present as a blunt bump between 25 and 32 mm, and is absent in specimens >32 mm long. The second superior infraorbital spine is occasionally present between 16 and ≈30 mm and is absent in larger and smaller specimens. The third superior infraorbital spine is usually present in specimens ≈13-31 mm and usually absent in other sized specimens. The fourth superior infraorbital spine is usually present as a sharp spine in specimens <32 mm, as a sharp spine or blunt bump between 32 and 41 mm, and is usually absent in specimens >41 mm. The nasal spine appears as a bump between 11 and 12 mm and as a sharp spine in all specimens >12 mm.

The tympanic spine appears as a blunt bump between ≈28 and 35 mm and usually as a small sharp spine in specimens >35 mm. The pterotic spine is present as a sharp spine in all specimens <25 mm, as a blunt bump in specimens 25-37 mm, and is absent in specimens >37 mm. The inferior posttemporal spine is present in all specimens of the series. The supracleithral spine appears at ≈12 mm and is present in all larger specimens. The superior posttemporal spine appears as a blunt bump at ≈16 mm and as a sharp spine in all specimens >17 mm. The cleithral spine is present in most specimens >40 mm as a weak, flexible spine.

Scale formation.—Lateral line organs, indicated by a row of light colored spots on the flesh, are visible on the smallest larva and on most larger larvae which lack scales. Developing scales are first visible on unstained specimens at ≈22 mm in the region above the pectoral fin, near the posttemporal and supracleithral spines. The body is scale covered by ≈26 mm.

TABLE 4.—Development of spines in the head region of *Sebastes entomelas* larvae and juveniles. Specimens

Standard length (mm)	Parietal	Nuchal	Preopercular								Opercular		Interopercular	Subopercular	Preocular	Supraocular	Postocular
			Anterior			Posterior											
			1st	2d	3d	1st	2d	3d	4th	5th	Superior	Inferior					
9.9	+	+	+	–	+	(1)	+	+	+	–	(1)	–	–	–	–	–	+
10.0	+	(1)	+	–	+	(1)	+	+	+	–	(1)	–	–	–	–	–	+
10.9	+	+	+	–	+	+	+	+	+	–	+	–	(1)	–	–	–	+
11.0	+	+	+	–	+	+	+	+	+	(1)	+	–	(1)	–	–	–	+
11.9	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
12.0	+	(1)	+	+[2]	+	(1)	+	+	+	(1)	(1)	–	(1)	–	–	–	+
12.9	+	+	+	–	+	+	+	+	+	+	(1)	–	(1)	–	–	–	+
13.7	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
14.0	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
14.9	+	+	+	–	+	+	+	+	+	+	+	–	(1)	–	–	–	+
15.2	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
16.2	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
16.8	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
17.7	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	–	+
18.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	(1)	+
18.5	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
19.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	(1)	+
20.4	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
20.8	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
21.0	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	(1)	+
[3]21.7	+	+	+	–	+	+	+	+	+	+	+	(1)	(1)	–	–	+	+
[3]22.3	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]22.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]23.9	+	+	+	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]24.5	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]24.5	+	+	+	–	+	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]25.3	+	–	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]25.9	+	+	+	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]26.5	+	+	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]26.7	+	+	(1)	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]27.2	+	+	+	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]27.9	+	+	(1)	–	(1)	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]28.5	+	+	–	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]29.1	+	+	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]29.7	+	+	(1)	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[3]30.6	+	+	–	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[5]30.8	+	+	–	–	–	+	+	+	+	+	+	+	+	–	(1)	+	+
[5]31.6	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]32.0	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]33.4	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]35.7	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]36.8	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[5]40.1	+	+	–	–	–	+[6]	+	+	+	+	+	+	+	–	+	+	+
[7]45.0	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]47.7	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	–[9]	+
[7]55.5	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]55.7	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]64.4	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	–	+	+	+
[7]65.0	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	+	(1)	+	+	+
[7]66.1	+[8]	+[8]	–	–	–	(1)	+	+	+	+	+	+	+	+	+	+	+
[7]71.2	+[8]	+[8]	–	–	–	–[6]	+	+	+	+	+	+	+	(1)	+	+	+
[7]74.1	+[8]	+[8]	–	–	–	–[6]	+	+	+	+	+	+	+	+	+	+	+
[7]74.5	+[8]	+[8]	–	–	–	+[6]	+	+	+	+	+	+	(1)	(1)	+	+	+

[1]Bump, indicating beginning of spine formation or last stage before spine is overgrown.
[2]– on the right side.
[3]Transforming.
[4]Spine is bifid.
[5]Pelagic juvenile.
[6]Spine tip directed posteriorly.
[7]Benthic juvenile.
[8]Parietal and nuchal spines fused, only one tip visible.
[9]+ on the right side.

Pigmentation.—The smallest larval *S. entomelas* has melanistic pigment on the head over the brain. Melanophores are present on the inside tip of the lower jaw, along the anterior margin of the maxillary, around the pterotic and posttemporal spines, and on the operculum. An internal melanistic shield covers the gut appearing darkest on the dorsal surface. Melanophores are present dorsally on the nape, beneath the posterior one-third of the spinous dorsal fin, beneath the soft dorsal fin, and along the dorsal surface of the caudal peduncle. Internal and external melanophores are present on the lateral midline of the caudal peduncle in the vicinity of notochord flexure, above the posterior portion of the anal fin, and along the ventral margin of the caudal peduncle. Melanophores line the margin of the hypural elements. The pectoral and pelvic fin blades are moderately pigmented with expanded, somewhat elongated melanophores. External and a few internal melanophores are

above dashed line are undergoing notochord flexion. + denotes spine present and − denotes spine absent.

Standard length (mm)	Infraorbital							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
9.9	+	−	−	+	−	−	+	−	−	−	+	−	+	−	−
10.0	(1)	−	−	+	−	−	(1)	−	−	−	+	−	+	−	−
10.9	+	+	−	+	−	−	(1)	−	−	−	+	−	+	−	−
11.0	+	−	−	+	−	−	−	(1)	−	−	+	−	+	−	−
11.9	+	+	−	+	−	−	+	(1)	−	−	+	−	+	+	−
12.0	+	+	−	+	−	−	+	(1)	−	−	+	−	+	+	−
12.9	+	+	−	+	−	−	+	+	−	−	+	−	+	+	−
13.7	+	+	−	+	−	+	+	+	−	−	+	−	+	+	−
14.0	+	+	−	+	−	+	+	+	−	−	+	−	+	+	−
14.9	+	+	+	+	−	+	+	+	−	−	+	−	+	+	−
15.2	+	+	+	+	−	+	+	+	−	−	+	−	+	+	−
16.2	+	+	+	+	−	+	+	+	−	−	+	(1)	+	+	−
16.8	+	+	+	+	+	+	+	+	−	−	+	(1)	+	+	−
17.7	+	+	+	+	+	+	+	+	−	−	+	+	+	+	−
18.4	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
18.5	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
19.4	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
20.4	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
20.8	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
21.0	+	+	+	+	+	+	+	+	−	−	+	+	+	+	−
21.7	+	+	+	+	+	+	+	+	−	−	+	+	+	+	−
22.3	+	+	+	+	+	+	+	+	−	−	+	+	+	+	−
22.9	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
23.9	+	+	+	+	−	+	+	+	−	−	+	+	+	+	−
24.5	+	+	+4	+	+	+	+	+	−	−	(1)	+	+	+	−
24.5	+	+	+	+	+	+	+	+	−	−	+	+	+	+	−
25.3	+	+	+	+	−	(1)	+	+	−	−	+	+	+	+	−
25.9	+	+	+	(1)	−	(1)	+	+	−	−	+	+	+	+	−
26.5	+	+	+	(1)	+	+	+	+	−	−	(1)	+	+	+	−
26.7	+	+	+	(1)	+	+	+	+	−	−	(1)	+	+	+	−
27.2	+	+	+	(1)	+	+	+	+	−	−	+	+	+	+	−
27.9	+	+	+	(1)	+	+	+	+	−	(1)	+	+	+	+	−
28.6	+	+	+	(1)	+	+	+	+	−	(1)	(1)	+	+	+	−
29.1	+	+	+4	(1)	−	+	+	+	−	(1)	(1)	+	+	+	−
29.7	+	+	+	(1)	+	+	+	+	−	(1)	(1)	+	+	+	−
30.6	+	+	+	(1)	−	−	(1)	+	−	(1)	(1)	+	+	+	−
30.8	+	+	+4	(1)	−	+	+	+	−	(1)	(1)	+	+	+	−
31.6	+	+	+	(1)	−	−	+	+	−	(1)	(1)	+	+	+	−
32.0	+	+	+	(1)	−	−	(1)	+	−	(1)	(1)	+	+	+	−
33.4	+	+	+	−	−	−	(1)	+	−	(1)	(1)	+	+	+	−
35.7	+	(1)	(1)	−	−	−	+	+	−	(1)	−	+	+	+	−
36.8	+	+	+	−	−	(1)	+	+	−	+	(1)	+	+	+	−
40.1	+	+	+	−	−	−	+	+	−	+	−	+	+	+	(1)
45.0	+	−	(1)	−	−	−	−	+	−	+	−	+	+	+	+
47.7	+	(1)	(1)	−	−	−	−	+	−	(1)	−	+	+	+	+
55.5	(1)	(1)	(1)	−	−	−	(1)	+	−	+	−	+	+	+	+
55.7	(1)	(1)	−	−	−	−	−	+	−	+	−	+	+	+	+
64.4	−	−	−	−	−	−	−	+	−	+	−	+	+	+	+
65.0	−	−	(1)	−	−	−	−	+	−	+	−	+	+	+	+
66.1	−	−	−	−	−	−	−	+	−	+	−	+	+	+	+
71.1	−	−	−	−	−	−	−	+	−	+	−	+	+	+	+
74.1	−	−	−	−	−	−	−	+	−	+	−	+	+	+	−
74.5	−	−	−	−	−	−	−	+	−	+	−	+	+	+	−

present on the underside of the pectoral fin base. A discrete melanophore is present at the articulation of each of several dorsal fin rays near the center of the soft dorsal fin.

As larvae develop, pigment increases over the brain. Melanophores are added on the snout, interorbital region, tips of the upper and lower lips, along the maxillary, and on the cheek and operculum. Pigment increases around the orbit and around the posttemporal spine, extending anteriorly over the head. Melanophores line the anterior margin of the cleithrum beneath the operculum. Pigment on the gut becomes less obvious as body musculature increases. The dorsal body surface is pigmented from nape to caudal peduncle by ≈11 mm. Large stellate melanophores beneath the soft dorsal fin increase in number and are aligned along the muscles surrounding the dorsal pterygiophores. This is the densest pigmentation on larvae. Internal and external melanophores are added along the body midline anteriorly from the caudal peduncle forming a line along the notochord which extends to the head by ≈16.5 mm. Melanophores extend ventrolaterally from the

nape to the lateral midline by ≈16.5 mm and are added posteriorly along the dorsolateral body surface with development. The melanophores located above the posterior portion of the anal fin disappear by ≈18 mm. Discrete melanophores are added at the articulation of dorsal fin rays and spines until most soft rays have an associated melanophore by ≈14 mm and most spines have one by ≈19 mm. Melanophores are added along the caudal fin base, sometimes appearing as a line of pigment, and onto the fin membrane. Pigment decreases and then disappears on the pelvic fin and underside of the pectoral fin base by ≈18 mm and on the pectoral fin by ≈20 mm.

During transformation, ≈22-31 mm, pigment gradually continues to increase over the head and body. External melanophores are added on the lips, lower jaw, snout, and dorsolateral areas of the head. Pigment becomes continuous around the orbit by ≈30 mm. Melanophores over the dorsolateral surfaces of the body often appear aligned along the myosepta, but this pattern becomes obscured as melanophores are added between the myosepta, particularly along the dorsal one-third of the body.

Pelagic juveniles, 31-40 mm, undergo a general increase in pigment with development. The upper head, snout, lips, lower jaw, maxillary, cheek, and gular region become increasingly pigmented with small melanophores. Melanophores are added ventrolaterally on the body until all but the ventral one-eighth is pigmented. Pigment distinctly lines the caudal fin base.

Benthic juveniles, >44 mm, become increasingly pigmented as small melanophores are added on the head and appear on the scales and fins. Pigmentation at the anterior tips of the lips and along the maxillary intensifies. By ≈55.5 mm a dark bar of pigment extends the length of the maxillary, and two other bars extend from the posteroventral margin of the eye across the cheek. The most dorsal cheek bar extends completely across the opercle. Dark blotches appear on the dorsal surfaces of the body as scale-borne melanophores overlie the body pigment which developed during the transformation and pelagic juvenile stages. In small benthic juveniles these blotches appear as indistinct bands as melanophores are added ventrolaterally to them. However, a mottled pattern appears over the dorsal half of the body by ≈66 mm. Melanophores are added anteriorly and proximally on the first dorsal fin and are eventually scattered over the entire fin. A dark blotch develops in the posterior portion of the spinous dorsal fin by ≈45 mm and persists in the largest juveniles observed; however, as development proceeds the blotch becomes less intensely pigmented and more of a pigment fringe, rather than a blotch. The membranes of the spinous and soft dorsal fins and caudal fin become lightly covered with small melanophores by ≈56 mm. Also by ≈56 mm, a small patch of melanophores appears on the dorsal half of the pectoral fin ray bases and adjacent fin base.

Occurrence (Figures 4, 5).—Adult *S. entomelas* occur from Todos Santos Bay, Baja California, to Kodiak Island, Alaska (Miller and Lea 1972). Off Oregon they are reported to be most common on the continental shelf between 100 and 200 m depth

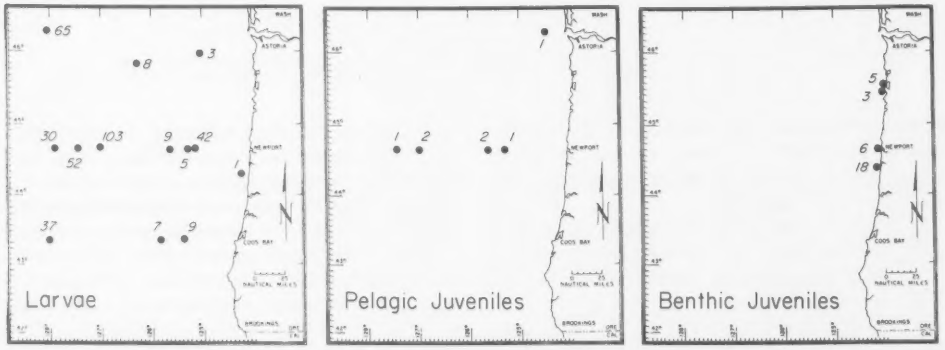

FIGURE 4.—Number of specimens and location of capture of larvae and juveniles of *Sebastes entomelas* off Oregon (1961-78) described in this paper.

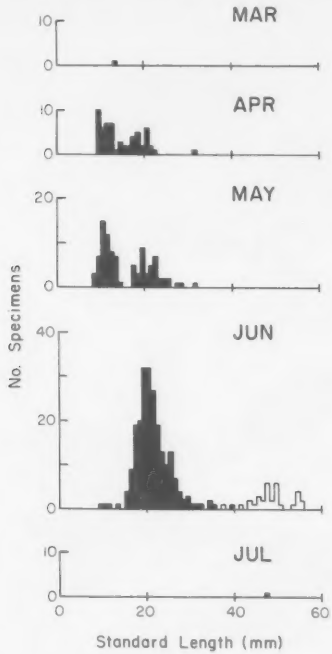

FIGURE 5.—Seasonal occurrence of larvae and juveniles of *Sebastes entomelas* off Oregon. Data from 1961 through 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

(Snytko and Fadeev[7]). Data from Niska (1976) show that ≈91% of the total Oregon trawl catch of *S. entomelas* landed from 1963 through 1971 was taken from depths of 110-218 m. Highest concentrations of *S. entomelas* found during the 1977 rockfish survey between Pt. Hueneme, Calif., lat. 34°00′ N, and Cape Flattery, Wash., lat. 48°29′ N, were at depths of 91-181 m between Cape Blanco, Oreg., lat. 43°00′ N, and Cape Flattery (Gunderson and Sample[8]). Larval and transforming *S. entomelas*, in our collections were captured at stations ≈9-306 km offshore. Pelagic juveniles appeared to range as extensively as larvae. Benthic juveniles were taken close to the coast at depths of 9-37 m.

Reported parturition times for *S. entomelas* are January through March off central California (Phillips 1958). Larvae <15 mm long were taken March through June, although most were taken in April and May. Larvae and pelagic juveniles >15 mm were taken April through June. Benthic juveniles were taken only in June. Lack of benthic juveniles in our collections from other months is probably due to inadequate sampling.

SEBASTES ZACENTRUS (GILBERT)

Literature (Figures 6-8).—The pigment pattern of *S. zacentrus* preextrusion larvae was described by Efremenko and Lisovenko (1970), including a figure; Westrheim (1975); Westrheim et al.[9]; and Harling et al. (footnote 6), including figures. Descriptions by Efremenko and Lisovenko (1970), Westrheim (1975), and Westrheim et al. (footnote 9) agree that preextrusion larvae (mean 4.2, 4.3, and 4.5 mm TL, respectively) have a postanal ventral row of melanophores (15-21, usually >16, and 15-20, respectively) which usually stops short of the anus by at least four myomeres with usually at least one melanophore in the hypural region. Melanophores also appear over the gut. No dorsal row of pigment is present. Harling et al. (footnote 6) described and illustrated two forms of *S. zacentrus* preextrusion larvae, both with mean 5.0 mm TL. One form had 15-18 ventral midline melanophores which stopped short of the anus by four myomeres, a hypural spot, and gut pigment. The second form had 18-21 ventral midline melanophores which did not stop short of the anus by four myomeres, 9-12 dorsal midline melanophores, considerable pigment encircling the yolk, a large lateral melanophore midway between the anus and tail tip, and several melanophores in the hypural region. It seems quite unlikely that the latter form is the same as the former and merely a result of within species variation as suggested by Harling et al. (footnote 6). Possibly it may reflect misidentification of the adult from which the larvae were taken. Since the two forms described by Harling et al. were consid-

[7]Snytko, V. A., and N. S. Fadeev. 1974. Data on distribution of some species of sea perches along the Pacific coast of North America during the summer-autumn seasons. Document submitted at the Canada-USSR meeting on fisheries in Moscow-Batumi, USSR-November 1974, 14 p. (Transl. 3436, Can. Transl. Ser.).

[8]Gunderson, D. R., and T. M. Sample. 1978. Distribution and abundance of rockfish off Washington, Oregon and California during 1977. Unpubl. rep., 45 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[9]Westrheim, S. J., W. R. Harling, D. Davenport, and M. S. Smith. 1968. Preliminary report on maturity, spawning season and larval identification of rockfishes (*Sebastodes*) collected off British Columbia in 1968. Fish. Res. Board Can., Manuscr. Rep. Ser. 1005, 28 p.

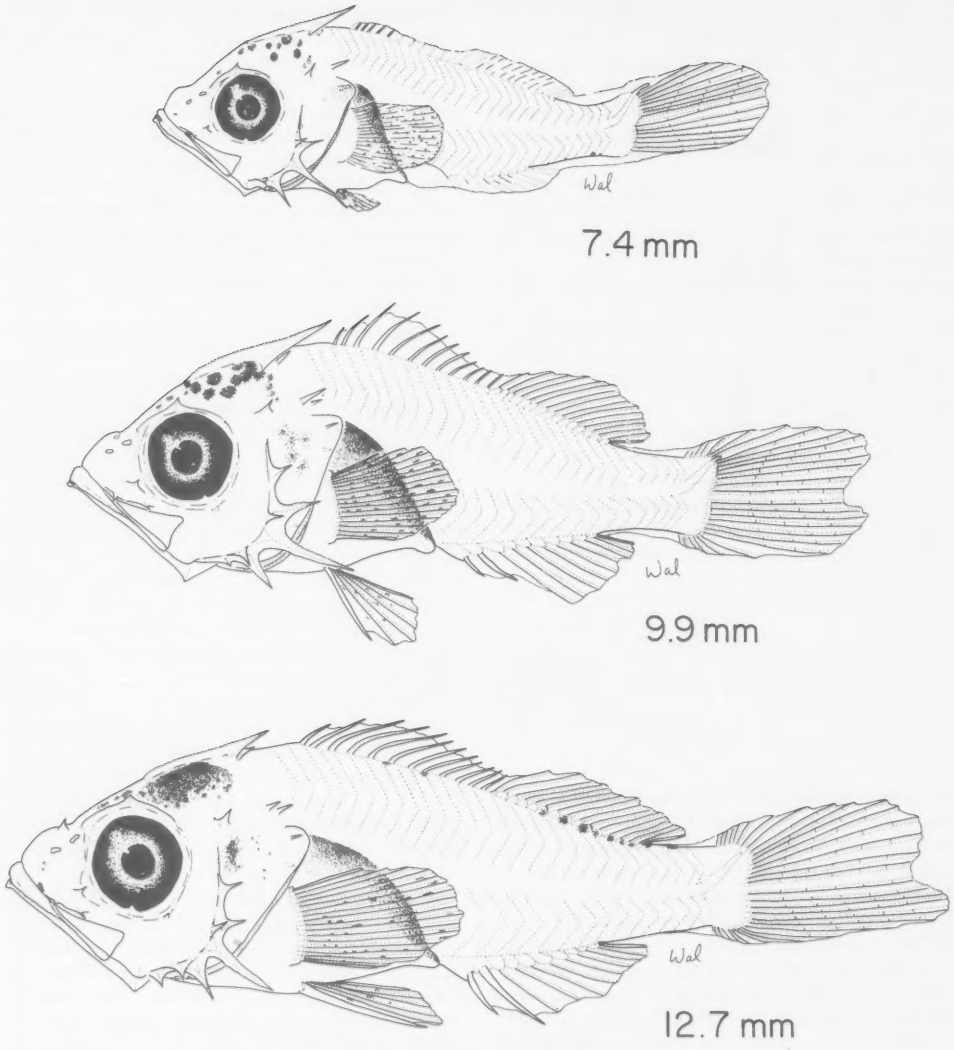

FIGURE 6.—Pelagic larvae of *Sebastes zacentrus*.

erably larger than those described by other workers (see above), there is some question about the identification of both.

Identification (Tables 5-7; Appendix Table 1).—Fifty-one specimens of *S. zacentrus* (7.4-74.8 mm) were selected for the developmental series from 181 larval and juvenile specimens identified. Juveniles were identified using the following combination of characters observed in juvenile and adult specimens examined:

Gill rakers = 32-37, usually 34-37
Lateral line pores = 38-48, usually 38-44

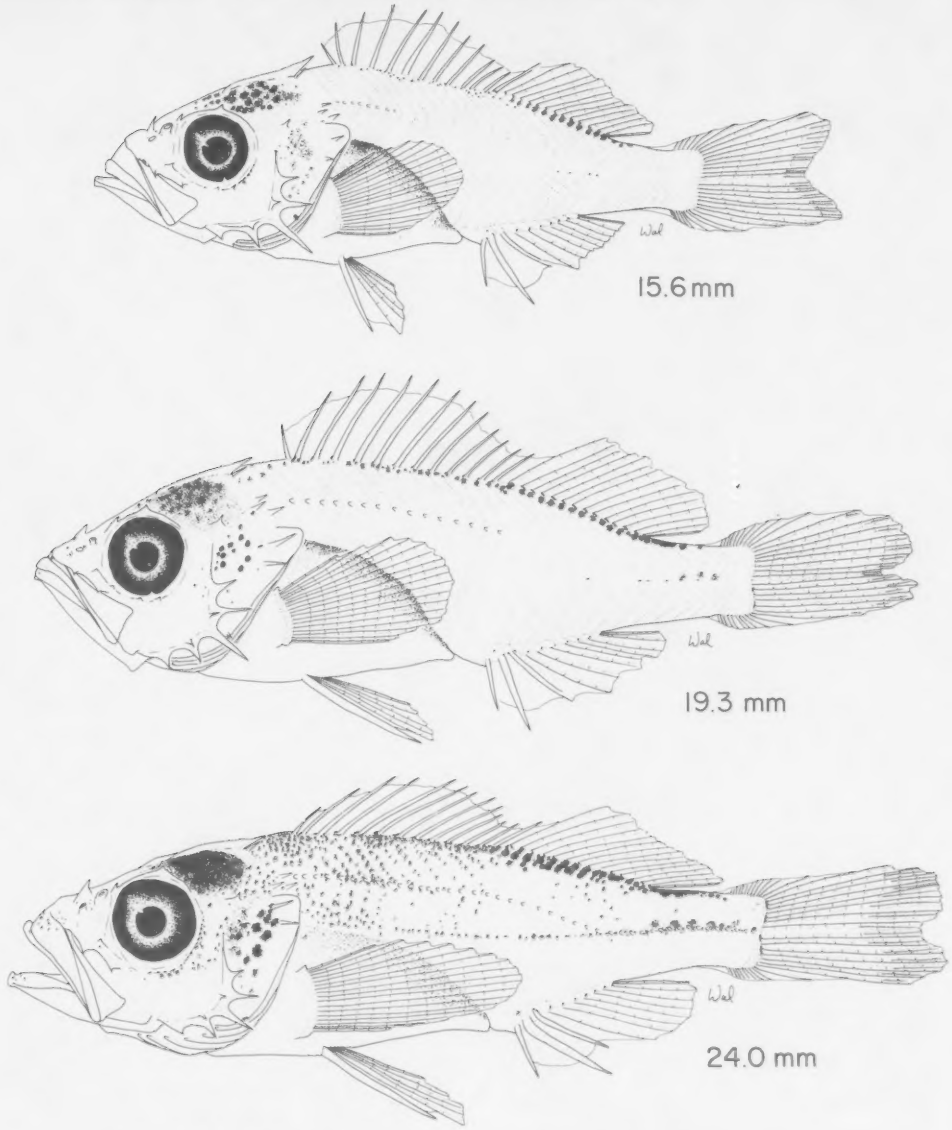

FIGURE 7.—Transforming larvae (15.6, 19.3 mm) and pelagic juvenile (24.0 mm) of *Sebastes zacentrus*.

Pectoral fin rays = 16-18, usually 17
Anal fin soft rays = 6 or 7, usually 7
Dorsal fin soft rays = 13-16, usually 14

Vertebrae = 27
Preocular spine = present (strong)
Supraocular spine = usually absent

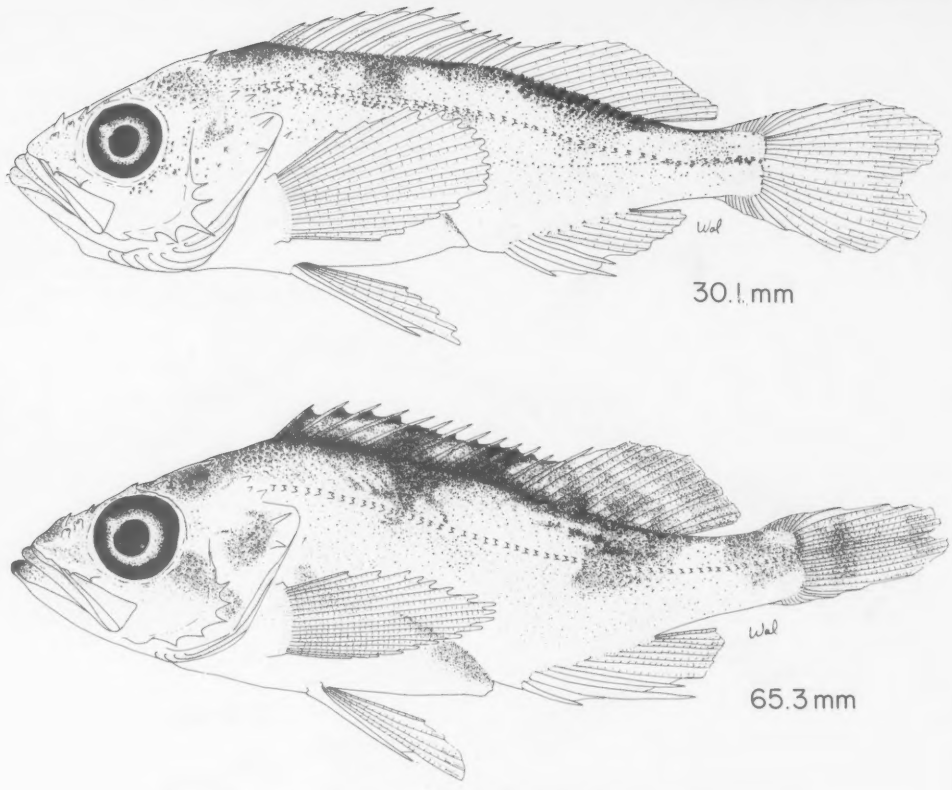

FIGURE 8.—Pelagic juvenile (30.1 mm) and benthic juvenile (65.3 mm) of *Sebastes zacentrus*.

Interorbital space = flat-convex
Black blotch at base of spinous dorsal fin = absent.

Of the 36 *Sebastes* species off Oregon (Richardson and Laroche 1979), *S. zacentrus* has the best fit to the above characters. Other species occurring off Oregon which agree with many of these characters are *S. brevispinis*, *S. emphaeus*, *S. proriger*, and *S. wilsoni*.

Sebastes emphaeus and *S. wilsoni* are eliminated since they have 39-43 and 38-42 gill rakers, respectively (see Appendix Table 1). *Sebastes wilsoni* also differs from *S. zacentrus* in soft anal fin ray count, usually 6 vs. usually 7, respectively (see Appendix Table 1). *Sebastes proriger* can be eliminated based on count frequency distributions (see Appendix Table 1): number of gill rakers on the first arch $\bar{x} = 38.3 \pm 0.35$ (95% confidence intervals, C. I.) vs. 35.3 ± 0.32 (95% C. I.) for *S. zacentrus*; diagonal scale rows below the lateral line $\bar{x} = 56.0 \pm 0.82$ (95% C. I.) vs. 50.2 ± 0.56 (95% C. I.) for *S. zacentrus*; lateral line pores $\bar{x} = 47.9 \pm 0.93$ (95% C. I.) vs. 41.8 ± 0.70 (95% C. I.) for *S. zacentrus*. Frequency distributions for dorsal fin soft rays also differ between *S. proriger*, 50% $\geq$15 rays, and *S. zacentrus*, 88% <14 rays. Although *S. brevispinis* differs considerably from *S. zacentrus* in body morphology, pigmentation, and relative strength and length of head and fin spines, the fin, scale, and lateral line pore count ranges are reported to overlap (Phillips 1957; Miller and Lea 1972; Hart 1973). Since count-frequency data have not been published for *S. brevispinis* and since we had only four large juvenile and adult specimens available for examination, it was necessary to rely on a

TABLE 5.—Meristics from larvae and juveniles of *Sebastes zacentrus* based on unstained specimens. Counts of left and right pelvic fin rays (I,5; I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7,7) were constant throughout the series. Specimens above dashed line are undergoing notochord flexion.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
7.4	V+I[1],14	III[1],7	17	17	—	—	—	—	—	—
7.9	XIII[1],13	III[1],7	17	17	18+ 7=25	17+ 7=24	—	—	—	—
8.5	XIII[1],14	III[1],7	17	17	18+ 8=26	19+ 8=27	—	—	—	—
9.2	XIII[1],14	III[1],7	17	17	20+ 8=28	19+ 8=28	—	—	—	—
9.9	XIII[1],14	III[1],7	17	17	20+ 9=29	21+ 9=30	—	—	—	—
10.1	XIII[1],14	III[1],7	16	17	21+ 9=30	21+ 8=29	—	—	—	—
10.6	XIII[1],14	III[1],7	17	17	22+ 8=30	21+ 9=30	—	—	—	—
11.2	XIII[1],14	III[1],7	17	17	21+ 9=30	21+ 9=30	—	—	—	—
11.7	XIII[1],14	III[1],7	18	17	21+ 9=30	23+ 9=32	—	—	—	—
12.4	XIII[1],13	III[1],7	17	17	22+ 9=31	22+10=32	—	—	—	—
12.7	XIII[1],14	III[1],7	17	17	24+ 9=33	23+ 9=32	—	—	—	—
13.3	XIII[1],14	III[1],7	17	17	23+ 9=32	22+ 9=31	—	—	—	—
[2]13.7	XIII,15	III[1],7	17	17	23+ 9=32	24+ 9=33	—	—	—	—
[2]14.0	XIII[1],14	III[1],6	18	17	24+ 9=33	24+ 9=33	—	—	—	—
[2]14.8	XIII[1],14	III[1],7	17	17	23+ 9=32	23+10=33	—	—	—	—
[2]15.0	XIII[1],14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]15.6	XIII,13	III[1],7	17	17	23+ 9=32	23+ 9=32	—	—	—	—
[2]16.3	XIII,14	III[1],7	17	17	24+10=34	23+10=33	—	—	—	—
[2]16.8	XIII,14	III[1],7	17	17	23+10=33	23+10=33	—	—	—	—
[2]17.3	XIII,14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]17.9	XIII,14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]18.0	XIII,14	III[1],7	17	17	24+10=34	24+10=34	—	—	—	—
[2]18.9	XIII,14	III[1],7	17	17	25+10=35	24+10=34	—	—	—	—
[2]19.3	XIII,14	III[1],7	17	17	25+10=35	24+10=34	—	—	—	—
[2]19.6	XIII,14	III[1],7	17	17	26+10=36	25+10=35	—	—	—	—
[3]20.3	XIII,14	III,7	17	17	26+10=36	25+10=35	—	—	—	—
[3]20.6	XIII,14	III,7	17	17	24+10=34	25+10=35	—	—	—	—
[3]21.0	XIII,14	III,7	17	17	25+10=35	25+10=35	—	—	—	—
[3]21.5	XIII,14	III,7	18	17	24+10=34	24+10=34	—	—	—	—
[3]22.0	XIII,14	III,7	17	17	25+10=35	24+11=35	—	—	—	—
[3]22.6	XIII,14	III,7	17	17	25+10=35	25+10=35	—	—	—	—
[3]23.3	XIII,13	III,7	17	17	25+10=35	25+10=35	—	41	—	—
[3]23.5	XIII,14	III,7	17	17	25+10=35	25+11=36	—	43	—	—
[3]24.0	XIII,14	III,7	17	17	26+10=36	25+10=35	—	43	—	—
[3]24.4	XIII,14	III,7	17	18	25+11=36	25+10=35	—	42	—	—
[3]25.6	XIII,14	III,7	17	18	24+10=34	25+10=35	42	—	52	—
[3]25.9	XIII,14	III,7	17	17	25+10=35	26+10=36	—	—	—	—
[3]26.3	XIII,14	III,7	17	17	24+10=34	25+10=35	43	41	48	50
[3]26.6	XIII,14	III,7	17	17	24+10=34	25+10=35	40	—	—	—
[3]27.6	XIII,14	III,7	17	17	25+10=35	24+10=34	—	—	—	—
[3]28.3	XIII,14	III,7	17	17	26+10=36	26+10=36	40	40	—	—
[3]30.1	XIII,14	III,7	17	17	25+10=35	25+10=35	42	41	—	—
[3]30.7	XIII,14	III,7	17	17	25+10=35	25+10=35	—	41	—	52
[3]31.2	XIII,14	III,7	17	17	25+10=35	24+10=34	40	—	—	—
[3]33.7	XIII,14	III,7	17	17	24+10=34	25+10=35	40	40	—	—
[3]35.3	XIII,14	III,7	17	17	25+10=35	25+10=35	44	43	—	—
[4]65.0	XIII,14	III,7	17	17	25+10=35	26+10=36	44	45	—	—
[4]65.3	XIII,13	III,7	17	16	25+10=35	26+10=36	41	43	—	—
[4]70.8	XII,14	III,7	17	17	24+10=34	26+10=36	44	43	—	—
[4]73.7	XIII,13	III,7	17	17	26+11=37	25+11=36	43	47	—	—
[4]74.8	XIII,14	III,7	17	17	24+10=34	24+10=34	43	42	—	—

[1]Posteriormost dorsal or anal spine appears as a soft ray.
[2]Transforming.
[3]Pelagic juvenile.
[4]Benthic juvenile.

number of characters for elimination of *S. brevispinis*. Characters useful for separating *S. brevispinis* from *S. zacentrus* are: weak or absent vs. strong supraorbital spines; 58-70 vs. 43-54 diagonal scale rows below the lateral line; 44-53 vs. 38-48, usually 38-44, lateral line pores; 26 vs. 27 vertebrae and myomeres; second anal spine about equal in strength and length to the third anal spine vs. second anal spine stouter and longer than the third anal spine. Larvae and small juveniles of 16 specimens, 14.9-28.1 mm, identified as *S. brevispinis* were found to have denser melanistic pigment over the head and body than *S. zacentrus* of similar length and more slender bodies at the pectoral fin base, averaging 26.1, 24.6, and 26.8% SL for larvae, transforming larvae, and pelagic juveniles vs. 35.2, 34.4, and 32.5% SL for comparable stages of *S. zacentrus*.

Distinguishing Features.—Characters useful to distinguish the smallest identified *S. zacentrus* larva, 7.4 mm, are fin counts; the moderately pigmented pectoral and pelvic fins; the general lack of body pigment; melanophores inside the tip of the

TABLE 6.—Measurements (millimeters) of larvae and juveniles of *Sebastes zacentrus*. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal-hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
7.4	9.1	4.0	3.1	0.92	1.4	1.0	0.86	2.5	1.7	0.80	1.2	0.95	0.98	0.48	0.88	2.9	0.82	0.04	0.84	—	0.19	0.69	(4)
7.9	10.0	4.0	3.1	0.72	1.4	1.1	0.98	2.8	2.0	0.92	1.3	1.2	1.1	0.90	1.2	3.0	0.76	(5)	1.2	0.26	0.52	1.0	0.40
8.5	10.9	4.5	3.8	0.98	1.8	1.2	1.1	3.1	2.2	1.1	1.3	1.5	1.0	—	1.2	3.3	0.64	0.12	—	0.40	0.54	0.76	0.54
9.2	11.8	5.2	4.2	1.1	1.8	1.3	1.2	3.3	2.5	1.0	1.4	1.9	1.1	1.3	1.5	3.8	—	0.22	—	0.55	0.90	1.2	0.70
9.9	12.8	5.6	4.4	1.2	1.7	1.4	1.2	3.5	2.6	1.1	1.5	2.0	1.1	1.4	1.5	4.2	0.76	0.20	0.98	0.58	0.92	1.2	0.78
10.1	13.0	5.6	4.2	1.1	1.8	1.4	1.3	3.4	2.6	1.0	1.5	2.1	1.1	1.4	1.6	4.1	0.68	0.24	1.1	0.52	1.0	1.4	0.88
10.6	13.3	5.7	4.4	1.3	2.0	1.5	1.2	3.6	2.7	1.2	1.6	2.2	1.1	1.6	1.9	4.2	0.75	0.10	1.3	0.48	1.1	1.2	0.92
11.2	14.4	6.4	4.6	1.3	2.1	1.6	1.3	4.0	3.0	1.3	1.7	2.4	1.1	1.8	1.9	4.7	0.66	0.21	1.2	0.68	1.3	1.7	1.2
11.7	14.9	6.8	5.3	1.5	—	1.5	1.3	4.0	3.0	1.3	1.6	2.4	1.2	1.9	2.0	4.9	0.66	0.30	1.3	0.72	1.3	1.5	1.1
12.4	15.9	7.0	5.4	1.5	2.4	1.7	1.5	4.3	3.4	1.4	1.6	2.8	1.3	2.4	2.6	4.9	0.64	0.28	1.2	0.73	1.7	1.8	1.7
12.7	16.2	7.2	5.1	1.4	2.3	1.7	1.5	4.2	3.1	1.4	1.8	3.0	1.3	2.2	2.4	4.8	0.64	0.29	1.3	0.72	—	1.6	—
13.3	16.9	8.3	5.4	1.6	2.4	1.6	1.5	4.4	3.1	1.4	1.9	3.0	1.3	2.2	2.4	5.4	0.68	0.40	1.4	0.78	1.6	1.8	1.3
[6]13.7	17.0	8.5	5.9	1.7	2.3	1.7	1.5	4.6	3.5	1.5	1.8	3.2	1.3	2.6	2.6	5.5	0.62	0.30	—	0.90	1.7	2.0	1.8
[6]14.0	17.9	8.0	5.4	1.5	2.5	1.6	1.6	4.9	3.9	1.5	2.2	3.4	1.4	2.9	3.0	5.7	0.76	0.32	1.4	0.87	1.9	—	1.8
[6]14.8	18.9	8.9	6.1	1.6	2.6	1.6	1.7	5.1	4.2	1.7	2.3	3.6	1.4	2.9	3.0	5.7	0.70	0.38	1.4	0.91	—	—	2.0
[6]15.0	18.0	8.8	6.1	1.5	2.6	1.7	1.5	5.1	4.0	1.6	2.2	3.7	1.4	3.0	3.1	5.9	0.70	0.37	1.5	0.88	—	—	2.1
[6]15.6	19.7	9.3	6.6	1.9	2.4	1.8	1.7	5.2	4.1	1.7	2.4	3.7	1.5	—	—	6.7	—	0.30	—	0.89	—	2.3	—
[6]16.3	20.8	10.0	6.6	1.6	2.8	2.1	1.7	5.1	4.3	1.7	2.4	4.1	1.6	3.0	3.0	7.3	0.62	—	1.5	0.96	2.4	2.6	2.3
[6]16.8	21.0	10.2	6.6	1.9	—	1.9	1.7	5.1	4.2	1.7	2.5	3.6	1.5	—	3.0	6.8	0.78	—	—	0.94	2.4	2.6	2.3
[6]17.3	—	10.8	6.9	1.7	2.7	2.0	1.7	5.4	4.4	1.9	2.5	4.4	1.5	—	—	7.4	0.64	0.22	1.6	1.1	—	2.5	2.3
[6]17.9	22.7	11.0	7.4	1.9	3.1	2.2	1.7	5.8	4.7	1.9	2.6	4.9	1.7	3.6	3.7	7.4	0.70	0.34	1.6	1.2	2.8	3.1	2.8
[6]18.0	22.8	11.1	7.5	1.9	3.2	2.3	1.8	5.7	4.5	2.0	2.7	4.9	1.7	3.7	3.9	7.4	—	—	1.2	1.1	2.9	2.9	3.0
[6]18.9	—	11.8	7.1	1.8	3.1	2.3	1.7	6.1	4.8	1.9	2.8	5.0	1.7	3.7	3.8	7.2	—	0.36	1.5	1.1	2.8	—	—
[6]19.3	24.4	11.0	7.5	1.9	3.0	2.3	2.0	6.0	4.9	1.9	2.7	5.1	1.7	3.6	—	7.7	0.58	0.32	—	1.1	2.9	—	—
[6]19.6	25.2	11.9	7.7	2.1	3.0	2.3	1.8	6.1	5.0	2.0	2.8	5.5	1.8	4.0	4.1	7.9	0.70	0.39	—	1.3	2.9	3.3	3.2
[7]20.3	25.6	12.0	8.1	2.1	3.4	2.3	1.9	6.3	5.1	2.1	3.0	5.4	1.8	—	4.2	8.1	0.66	0.37	1.4	1.3	3.1	3.0	—
[7]20.6	25.6	12.1	7.7	1.9	3.4	2.4	1.8	6.3	5.2	2.0	3.4	5.2	1.9	4.1	4.1	8.1	0.70	0.42	1.5	1.2	3.2	—	3.2
[7]21.0	25.7	13.2	8.4	2.1	3.6	2.4	2.0	6.3	5.0	2.0	2.8	6.1	1.9	—	—	8.4	0.62	0.34	1.2	1.4	3.6	—	3.3
[7]21.5	26.9	12.6	8.6	2.7	—	2.3	2.0	6.5	5.2	2.1	2.8	5.4	2.0	4.2	4.2	8.7	0.92	0.48	—	1.3	—	—	3.4
[7]22.0	—	13.5	8.5	2.5	3.2	2.5	1.8	6.8	5.3	2.1	2.9	—	1.9	—	—	9.3	0.57	0.30	—	1.2	3.2	—	3.3
[7]22.6	28.4	13.6	8.6	2.1	3.9	2.6	2.0	6.9	5.7	2.3	3.4	—	2.1	4.2	4.1	8.6	—	—	1.4	1.4	3.6	—	3.7
[7]23.3	29.6	13.9	9.0	2.4	3.6	2.6	1.9	6.7	5.5	2.2	3.2	6.3	2.1	4.2	4.7	9.2	—	—	1.5	1.2	3.6	3.6	3.7
[7]23.5	—	14.3	8.7	2.1	3.5	2.5	2.0	7.1	6.0	2.4	3.3	6.3	2.1	4.7	4.7	9.2	—	0.44	1.5	1.4	—	—	3.6
[7]24.0	30.5	14.8	9.7	2.7	4.0	2.9	2.0	7.2	5.9	2.4	3.6	6.6	2.2	4.2	4.7	9.7	—	0.32	—	1.4	3.5	3.6	—
[7]24.4	—	14.0	9.5	2.5	4.0	2.8	2.1	7.8	6.3	2.1	3.5	6.1	2.4	—	—	9.4	0.52	0.30	—	1.4	—	3.6	3.6
[7]25.6	32.0	16.4	9.4	2.5	4.0	2.8	2.1	7.7	6.0	2.4	3.9	6.8	2.2	4.3	4.9	10.4	0.36	0.24	1.0	1.5	3.6	4.0	3.9
[7]25.9	32.1	15.7	10.1	2.7	3.6	2.8	2.1	7.7	6.1	2.5	3.5	6.7	2.3	4.6	4.9	10.3	—	0.42	1.1	1.5	3.6	4.2	3.8
[7]26.3	32.7	15.6	9.6	2.7	4.0	2.8	2.1	8.3	6.6	2.5	3.6	—	2.3	4.6	5.1	10.4	0.38	0.24	—	1.5	3.6	4.0	4.3
[7]26.6	—	16.3	9.5	2.7	3.6	2.8	2.1	8.1	6.5	2.6	3.3	7.2	2.3	4.3	—	10.4	—	0.15	—	1.4	3.4	—	4.0
[7]27.6	34.7	16.3	10.0	2.2	4.2	3.1	2.1	7.8	6.6	2.7	3.9	7.5	2.4	—	5.8	10.0	—	0.16	—	1.5	3.8	—	4.3
[7]28.3	34.9	17.5	10.4	2.8	—	2.8	2.1	8.5	7.0	2.6	3.6	—	2.4	4.9	5.4	11.3	—	0.32	1.1	1.6	3.8	—	4.4
[7]30.1	37.4	18.6	10.9	2.7	4.6	3.1	2.2	9.2	7.1	3.0	4.4	8.6	2.7	4.6	6.1	11.9	—	0.36	—	1.7	4.2	4.5	4.7
[7]30.7	37.7	19.4	11.4	3.1	4.7	3.4	2.2	8.5	7.0	2.8	4.0	8.2	2.7	4.8	5.9	12.0	—	0.32	1.2	2.0	4.0	4.8	4.5
[7]31.2	39.1	19.2	11.5	2.7	5.0	3.5	2.2	9.4	7.3	2.9	4.6	8.8	2.6	—	6.2	12.0	—	0.30	0.82	1.9	3.9	5.2	4.8
[7]33.7	41.3	20.8	11.6	3.0	4.5	3.3	2.4	9.8	7.9	3.1	4.7	8.7	2.7	—	—	12.2	—	0.14	0.88	1.9	—	—	4.9
[7]35.3	42.6	22.3	12.3	3.1	4.6	3.4	2.4	10.3	8.5	3.4	4.8	8.8	2.8	—	6.1	14.6	—	0.24	0.82	1.8	—	5.2	—
[8]65.0	80.5	37.0	23.2	4.5	10.7	7.7	4.1	22.0	17.0	6.1	8.8	17.5	6.3	11.0	14.7	26.1	0.92	(9)	1.1	3.8	—	10.9	12.7
[8]65.3	79.7	40.0	23.4	4.3	10.0	7.5	4.0	20.7	16.4	6.3	9.0	17.2	6.3	10.4	14.5	27.0	0.60	(9)	1.2	3.8	9.4	10.8	12.0
[8]70.8	86.3	41.1	26.9	6.7	10.9	8.3	4.2	22.0	17.2	6.4	9.8	19.2	6.8	10.4	15.0	30.1	0.44	(9)	0.92	4.2	9.2	11.0	12.4
[8]73.7	89.7	43.5	27.8	7.0	11.7	8.1	4.6	23.5	19.6	7.0	10.6	18.7	7.5	11.4	15.0	29.7	0.46	(9)	1.0	4.4	10.5	12.2	12.9
[8]74.8	91.3	43.7	27.7	5.8	11.0	8.1	4.5	23.4	20.0	6.9	10.4	19.5	7.4	11.0	15.2	30.1	0.80	(9)	0.86	4.4	10.7	12.5	15.2

[1]Usually fourth or fifth.
[2]Usually midfin.
[3]The second spine.
[4]Forming.
[5]Bump.
[6]Transforming.
[7]Pelagic juvenile.
[8]Benthic juvenile.
[9]Nuchal spine overgrown.

lower jaw; narrow interorbital distance (27.7% HL); and long, deeply serrated, parietal spine (26.5% HL). Later stage larvae change little in overall appearance from the smallest larva, except for addition of melanophores along the dorsal body surface beneath the spinous and soft dorsal fins, along the dorsal surface of the caudal peduncle, and at the articulation of some dorsal soft fin rays of specimens >12.5 mm. A row of melanophores along the lateral midline and a strong, sharp preocular spine develop during the transformation period. Meristic characters, presence of a preocular and lack of a supraocular spine, the flat-convex shape and narrow width of the interorbital space, and stout, relatively long, second anal spine serve to distinguish pelagic and benthic juveniles.

General Development.—The smallest specimens (7.4-8.5 mm) of *S. zacentrus* are undergoing the

final stage of notochord flexion, which is completed by ≈9 mm. Transformation from postflexion larva to pelagic juvenile occurs between ≈13.5 and 20 mm as indicated by structural change of the dorsal and anal fin prespines to sharp, hard spines. Melanistic pigmentation gradually increases along the dorsal body surface under the dorsal fins and along the lateral midline of the caudal peduncle through the larval and transformation periods. A more rapid increase in pigment over the body, progressing anterior to posterior, is initiated at the beginning of the pelagic juvenile stage (≈20 mm). Transition from pelagic to benthic habitat takes place at lengths somewhere between 35 and 65 mm. The largest pelagic juvenile was 65.0 mm. Because of the long-term pelagic sampling effort off Oregon and the lack of specimens in the 35-65 mm length range, it seems likely that this species transforms at a relatively small size (≈35-40 mm). Small benthic juveniles would not be retained in the large mesh bottom trawls. The smallest benthic juvenile observed was 65.0 mm long.

Morphology (Tables 2, 6).—Various body parts were measured on 51 selected specimens of *S. zacentrus* (7.4-74.8 mm). Relative growth trends are summarized in Table 2.

This is a relatively deep-bodied form with body depth 35% SL in flexion larvae, decreasing to 30% in pelagic juveniles. It also has a rather large head, averaging 40-43% SL during the larval and transforming periods.

Fin Development (Tables 2, 5, 6).—The adult complement of 16-18, usually 17, pectoral fin rays is present in the smallest larva (7.4 mm). The pectoral fin is of moderate length, increasing from 15.3% SL in flexion larvae to 26.7 and 26.4% SL in pelagic and benthic juveniles, respectively.

The adult complement of pelvic fin spine and rays (I,5) is present on the smallest larva. The pelvic fin is moderately long increasing from 13.7 to 21.3% SL between flexion and benthic juvenile stages. The pelvic spine is also of moderate length, reaching 20% SL in transforming larvae.

The adult complement of 8+7 principal caudal fin rays can be counted on the smallest larva. Five benthic juveniles, ≈65-75 mm, had superior and inferior secondary caudal fin rays, respectively: 10/11 (three specimens) and 11/10 (two specimens), as determined from radiographs.

Dorsal fin spines and rays, including prespines, are completely formed by ≈8 mm but developing elements are countable in the smallest larva (7.4 mm). The dorsal and anal fin prespines become spines by ≈15.5 and 20 mm, respectively, marking the beginning of the pelagic juvenile stage.

Spination (Tables 2, 7).—Spines on the left side of the head of the smallest *S. zacentrus* include the parietal; nuchal; first and third anterior preopercular spines; first, second, third, fourth, and fifth (as a bump) posterior preopercular spines; superior opercular spine (as a bump); postocular; first inferior infraorbital; first superior infraorbital; pterotic; and the inferior posttemporal spine.

The parietal spine and ridge are serrated on all specimens <36 mm long. The relatively long (23% HL) parietal spine decreases in prominence to ≈3% HL by the benthic juvenile stage. The nuchal spine is always smaller than the parietal and is completely fused to it in benthic juveniles.

All five posterior preopercular spines are present as sharp spines by 8.5 mm and persist in adults. The third spine is relatively long (33% HL in flexion larvae) and decreases in length with development to 4% HL in benthic juveniles. Serrations are present on the first anterior preopercular spine of specimens <22 mm long, on the first and second posterior preopercular spines on specimens <26.5 mm, and on the third posterior preopercular spine to ≈34 mm. The first and third anterior preopercular spines are reduced to blunt bumps by ≈25 mm and are absent on all specimens >26.3 mm.

The superior opercular spine is sharp tipped by ≈8 mm. The inferior opercular spine appears as a blunt bump at ≈8 mm and becomes a sharp tipped spine by ≈13 mm. The interopercular spine appears as a blunt bump by ≈8 mm and as a small, sharp spine in all specimens >12 mm. The subopercular spine appears as a blunt bump by ≈13 mm, is usually present as a short, sharp spine between 13 and 23 mm, is reduced to a blunt bump on specimens 23-26 mm, and is usually absent on specimens >26 mm.

The ridge anterior to the postocular spine is serrated on specimens <27 mm. The preocular spine appears as a blunt bump at 14 mm and usually as a moderately strong, sharp spine on most specimens >15 mm. The first inferior infraorbital spine is present as a sharp spine on all specimens to 35 mm and as a blunt bump in the benthic juveniles examined (65.0-74.8 mm). The second

TABLE 7.—Development of spines in the head region of *Sebastes zacentrus* larvae and juveniles. Specimens

Standard length (mm)	Parietal	Nuchal	Preopercular									Opercular		Inter-opercular	Sub-opercular	Pre-ocular	Supra-ocular	Post-ocular
			Anterior			Posterior												
			1st	2d	3d	1st	2d	3d	4th	5th		Superior	Inferior					
7.4	+	+	+	–	+	+	+	+	+	(1)		(1)	–	–	–	–	–	+
7.9	+	(1)	+	–	+	+	+	+	+	(1)		+	–	(1)	–	–	–	+
8.5	+	+	+	–	+	+	+	+	+	+		+	(1)	(1)	–	–	–	+
9.2	+	+	+	–	+	+	+	+	+	+		+	(1)	(1)	–	–	–	+
9.9	+	+	+	–	+	+	+	+	+	+		+	(1)	(1)	–	–	–	+
10.1	+	+	+	–	(1)	+	+	+	+	+		+	(1)	(1)	–	–	–	+
10.6	+	+	+	–	+	+	+	+	+	+		+	(1)	(1)	–	–	–	+
11.2	+	+	+	–	+	+	+	+	+	+		+	(1)	–	–	–	–	+
11.7	+	+	+	–	+	+	+	+	+	+		+	(1)	+	–	–	–	+
12.4	+	+	+	–	+	+	+	+	+	+		+	(1)	(1)	–	–	–	+
12.7	+	+	+	–	+	+	+	+	+	+		+	+	(1)	(1)	–	–	+
13.3	+	+	+	–	+	+	+	+	+	+		+	+	+	+	–	–	+
[2]13.7	+	+	+	–	+	+	+	+	+	+		+	+	+	+	–	–	+
[2]14.0	+	+	+	–	+	+	+	+	+	+		+	+	+	+	–	–	+
[2]14.8	+	+	+	–	+	+	+	+	+	+		+	+	+	+	(1)	–	+
[2]15.0	+	+	+	–	+	+	+	+	+	+		+	+	+	+	(1)	–	+
[2]15.6	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[2]16.3	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[2]16.8	+	(1)	+	–	+	+	+	+	+	+		+	+	+	+	(1)	–	+
[2]17.3	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[2]17.9	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[2]18.0	+	+	+	–	+	+	+	+	+	+		+	+	+	–	+	–	+
[2]18.9	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[2]19.3	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[2]19.6	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]20.3	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]20.6	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]21.0	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]21.5	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]22.0	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]22.6	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]23.3	+	+	+	–	+	+	+	+	+	+		+	+	+	+	+	–	+
[3]23.5	+	+	+	–	+	+	+	+	+	+		+	+	+	(1)	+	–	+
[3]24.0	+	+	+	–	+	+	+	+	+	+		+	+	(1)	(1)	+	–	+
[3]24.4	+	+	+	–	(1)	+	+	+	+	+		+	+	+	(1)	+	–	+
[3]25.6	+	+	(1)	–	(1)	+	+	+	+	+		+	+	+	(1)	+	–	+
[3]25.9	+	+	(1)	–	+	+	+	+	+	+		+	+	+	(1)	+	–	+
[3]26.3	+	+	(1)	–	(1)	+	+	+	+	+		+	+	(1)	(1)	+	–	+
[3]26.6	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[3]27.6	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[3]28.3	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[3]30.1	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[3]30.7	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[3]31.2	+	+	–	–	–	+	+	+	+	+		+	+	(1)	(1)	+	–	+
[3]33.7	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[3]35.3	+	+	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[4]65.0	+[5]	+[5]	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[4]65.3	+[5]	+[5]	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[4]70.8	+[5]	+[5]	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[4]73.7	+[5]	+[5]	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	+
[4]74.8	+[5]	+[5]	–	–	–	+	+	+	+	+		+	+	(1)	–	+	–	(1)

[1]Bump, indicating beginning of spine formation or last stage before spine is overgrown.
[2]Transforming.
[3]Pelagic juvenile.
[4]Benthic juvenile.
[5]Parietal and nuchal spines fused, only one tip visible.

inferior infraorbital spine appears as a blunt bump at ≈8 mm and as a sharp spine in larger specimens. The first superior infraorbital spine is present as a sharp spine on all specimens <23 mm, as either a sharp spine or a blunt bump between 23 and 35 mm, and was absent in the benthic juveniles examined (65.0-74.8 mm). The second superior infraorbital spine is occasionally present between 15 and 30 mm. The third superior infraorbital spine is usually present as a sharp spine in larvae and pelagic juveniles 14 to 35 mm. Smaller larvae and benthic juveniles examined lacked this spine. The fourth superior infraorbital spine usually appears as a blunt bump in larvae 8-10 mm long and as a sharp spine in all larvae and pelagic juveniles >10 mm. This spine was absent in benthic juveniles. The nasal spine appears as a blunt bump in larvae ≈10-11 mm long and as a sharp spine in all larger specimens.

The tympanic spine appears as a blunt bump between 17 and 18 mm and as a sharp spine in all larger specimens. The pterotic spine is reduced to a blunt bump by 30 mm and is absent on benthic juveniles. The inferior posttemporal spine is pres-

above dashed lines are undergoing notochord flexion. + denotes spine present and – denotes spine absent.

Standard length (mm)	Infraorbital							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
7.4	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
7.9	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.5	+	(1)	–	+	–	–	(1)	–	–	–	+	–	+	+	–
9.2	+	+	–	+	–	–	+	–	–	–	+	–	+	+	–
9.9	+	+	–	+	–	–	(1)	(1)	–	–	+	–	+	+	–
10.1	+	+	–	+	–	–	(1)	(1)	–	–	+	–	+	+	–
10.6	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
11.2	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
11.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.3	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
213.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
214.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
214.8	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
215.0	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
215.6	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
216.3	+	+	–	+	+	+	+	+	–	–	+	–	+	+	–
216.8	+	+	–	+	+	+	+	+	–	(1)	+	–	+	+	–
217.3	+	+	–	+	+	+	+	+	–	(1)	+	(1)	+	+	–
217.9	+	+	–	+	+	+	+	+	–	(1)	+	–	+	+	–
218.0	+	+	–	+	(1)	+	+	+	–	(1)	+	+	+	+	–
218.9	+	+	–	+	(1)	+	+	+	–	+	+	(1)	+	+	–
219.3	+	+	–	+	+	+	+	+	–	+	+	+	+	+	–
219.6	+	+	–	+	(1)	+	+	+	–	+	+	+	+	+	(1)
320.3	+	+	–	+	(1)	+	+	+	–	+	+	+	+	+	(1)
320.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
321.0	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
321.5	+	+	–	+	–	+	+	+	–	+	+	+	+	+	(1)
322.0	+	+	–	+	–	+	+	+	–	+	+	+	+	+	–
322.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	–
323.3	+	+	–	(1)	+	+	+	+	–	+	+	+	+	+	+
323.5	+	+	–	(1)	–	+	+	+	–	+	+	+	+	+	+
324.0	+	+	–	(1)	–	+	+	+	–	+	+	+	+	+	(1)
324.4	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+
325.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
325.9	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+
326.3	+	+	–	+	+	+	+	+	–	+	+	+	+	+	+
326.6	+	+	–	+	+	+	+	+	–	+	+	+	+	+	(1)
327.6	+	+	–	+	–	+	+	+	–	+	+	+	+	+	+
328.3	+	+	–	(1)	–	+	+	+	–	+	+	+	+	+	+
330.1	+	+	–	+	(1)	+	+	+	–	+	(1)	+	+	+	+
330.7	+	+	–	(1)	–	+	+	+	–	+	(1)	+	+	+	+
331.2	+	+	–	(1)	–	–	+	+	–	+	(1)	+	+	+	+
333.7	+	+	–	(1)	–	(1)	+	+	–	+	(1)	+	+	+	+
335.3	+	+	–	(1)	–	+	+	+	–	+	(1)	+	+	+	+
465.0	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
465.3	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
470.8	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
473.7	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+
474.8	(1)	+	–	–	–	–	–	+	–	+	–	+	+	+	+

ent in all specimens examined. The supracleithral spine appears by ≈8 mm and is present as a sharp spine on all larger specimens. The superior posttemporal spine appears as a blunt bump at ≈17 mm and is present as a sharp spine on all specimens >19 mm long. The cleithral spine appears as a blunt bump at ≈20 mm and is usually present as a sharp spine in specimens >23 mm.

Scale Formation.—Lateral line organs, indicated by a row of light colored spots on the flesh, are visible on the smallest larva and most larger larvae before scales form. Developing scales are visible on unstained specimens at 19.6 mm in the region above the pectoral fin, near the posttemporal and supracleithral spines. The body is scale covered by ≈30 mm.

Pigmentation.—The smallest *S. zacentrus* larva has melanistic pigmentation on the head over the brain, inside the tip of the lower jaw, and along the anteroventral margin of the maxillary. Melanophores are densely concentrated on the dorsal surfaces of the gut and are present in lesser concentrations on the body wall over the gut cavity. Four small melanophores are present along the ventral midline of the caudal peduncle. The pectoral and pelvic fin membranes are covered with

moderately large and elongate melanophores. Melanophores are also present along the ventral margin and underside of the pectoral fin base.

As larvae develop, pigment increases on the head over the brain, and a few small melanophores may appear on the snout in larvae >12 mm. Melanophores appear on the opercle by ≈8 mm and increase in number with development. By ≈12 mm, melanophores appear just above the opercle near the pterotic and inferior posttemporal spines. About one-half of larvae observed have at least one melanophore along the anterior margin of the cleithrum beneath the opercle. Gut pigmentation remains intense through the larval period. Melanophores begin to appear on the nape and along the dorsal surface of the body beneath the spinous and soft dorsal fins by ≈12 mm. This pigmentation beneath the soft dorsal fin is composed of large, expanded melanophores and always appears as the most densely pigmented area on larvae. The small melanophores along the ventral midline of the caudal peduncle usually disappear by ≈10 mm; two specimens, 12.4 and 13.3 mm, had one and two melanophores in this region, respectively. A single larva (11.7 mm) had one melanophore on the margin of the hypural plate. The pectoral and pelvic fin membranes are usually pigmented in larvae although the intensity and number of melanophores decreases with development. By 12 mm, melanophores entirely disappear from the pectoral fin base.

Early in the transformation period (≈14-20 mm), melanistic pigmentation rapidly appears over the dorsal surfaces of the snout, head, nape, body, and caudal peduncle and then continues to increase gradually ventrolaterally with development. Melanophores appear on the cheek, posteroventral to the eye by 14 mm, and begin to extend around the posteroventral portion of the orbit by ≈16 mm. Melanophores extend from the nape anteriorly joining the head pigment and laterally toward the body midline at the same time that pigment extends ventrolaterally from beneath the spinous dorsal fin. By ≈16 mm, some melanophores appear aligned along the myosepta over the anterior one-fourth of the body but never appear very distinct. By ≈15.5 mm, internal and external melanophores appear along the lateral midline anterior to the point of notochord flexion and just posterior to the head on specimens greater than ≈16 mm. Melanophores appear along the margin of the hypural elements in most specimens >16 mm. A melanophore appears at the point of articulation of most dorsal fin rays on specimens >15 mm, occasionally of some anal rays on specimens 13.5-19 mm, and of most anal fin rays on all specimens >19 mm. Melanophores are usually absent on the pelvic fin membrane on transforming larvae. Specimens >14 mm usually lack melanophores on the pectoral fin membrane. A single larva (19.3 mm) had a few small melanophores near the anterior base of the spinous dorsal fin membrane.

Melanistic pigmentation continues to intensify and increase gradually on pelagic juveniles, 20-35 mm. Melanophores cover the dorsal surface of the head and appear at the tips of the upper and lower lips by ≈24 mm. By ≈28 mm, melanophores extend over the cheek and around the posterior half of the orbit which becomes completely encircled by pigment at ≈30 mm. Melanophores appear on the gular region by ≈30 mm. Internal and external melanophores form a continuous irregular row along the lateral body midline by ≈20 mm. Melanophores also cover the ventrolateral area anterior to the soft dorsal fin between the dorsal margin and the lateral midline. At ≈21 mm, the large, expanded melanophores under the soft dorsal become concentrated along muscles surrounding the dorsal pterygiophores giving the appearance of vertical lines of pigment. Pigmentation on the body and caudal peduncle extends nearly to the ventral surface on specimens >28 mm. Areas of somewhat intensified pigmentation extend posteroventrally from the nape and spinous and soft dorsal fin bases appearing as faint saddles. A few small melanophores are occasionally present along the anterior portion of the spinous dorsal fin membrane near its base on pelagic juveniles <35 mm. The largest pelagic juvenile (35.3 mm) has melanophores scattered over the proximal two-thirds of the spinous dorsal membrane. Small melanophores appear on the caudal fin near its base by ≈25 mm.

Benthic juveniles, 65.0-74.8 mm, have about the same pigment pattern as that of the largest pelagic juvenile. However, they are more darkly pigmented due to the addition of numerous small melanophores over most surfaces of the head, body, and fins. The added pigmentation over the upper areas of the head and opercle, and on the body results from development of melanophores borne on the scales and skin tissue surrounding the scale pockets. This pigmentation overlies the larval and pelagic juvenile pigment which persists on benthic juveniles most obviously beneath the soft

dorsal fin where large melanophores remain. Melanophores on the dorsal portion of the opercle increase in number and intensify appearing as a patch of darker pigment. A single bar of pigment extends from the posteroventral margin of the eye across the cheek and opercle. Five faint saddles extend, one from the nape, two under the spinous dorsal fin, one under the soft dorsal fin, and one across the caudal peduncle, ventrolaterally from the dorsal surface of the body to just beneath the lateral midline. Spinous and soft dorsal fin membranes are covered by small melanophores with bands of more intense pigmentation extending across the fins as extensions of the body saddles. The largest benthic juvenile (74.8 mm) also has moderately intense pigmentation along the distal edge of the spinous dorsal fin membrane, concentrated immediately posterior to each dorsal spine. The caudal fin of benthic juveniles is lightly covered by small melanophores with sometimes a slightly darker bar of pigment apparent in the proximal third of the fin. A few small melanophores are present on the proximal half of the anal fin membrane, and small melanophores lightly cover the proximal half of the dorsalmost pectoral fin rays and the adjacent pectoral fin base.

Occurrence (Figures 9, 10).—Adult *S. zacentrus* occur from San Diego, Calif., to the Sanak Islands, Alaska, lat. 54.13° N, long. 161.37° W (Miller and Lea 1972; Hart 1973). Data from Niska (1976) show that 95% of the total Oregon trawl catch of *S. zacentrus* landed from 1963 through 1971 was taken from depths of 181-416 m. Highest concentrations of *S. zacentrus* found during a rockfish survey in 1977 between Pt. Hueneme and Cape Flattery were at depths of 183-272 m between Cape Blanco and the Columbia River, lat. 43°00′-47°30′ N (Harling et al. footnote 7). Larval *S. zacentrus*, including transforming specimens, in our collections were captured at stations ranging from 46 to 148 km offshore, ≈270-2,800 m depth. The data seem to indicate a more restricted offshore distribution for *S. zacentrus* larvae than for some other rockfish species: i.e., *S. entomelas*, 9-306 km; *S. pinniger*, 13-306 km; *S. flavidus*, 24-266 km; and *S. melanops*, 5-266 km (Richardson and Laroche 1979; Laroche and Richardson 1980). This is of interest as presumably the morphology of *S. zacentrus*, i.e., large head spines, stubby and deep body, would tend to enhance larval transport as suggested for *S. pinniger* (Richardson and Laroche 1979). The more restricted offshore occurrence of larvae may reflect the season of occurrence and associated wind regimes which are from the south and towards the coast in fall and winter. This would tend to minimize offshore dispersal. Pelagic juveniles occurred in about the same offshore area, 9-148 km offshore, as larvae. All demersal juveniles were taken from a single otter trawl haul made ≈40 km offshore, 91 m depth.

Reported parturition time for *S. zacentrus* is July off Oregon (Westrheim 1975). Larvae <10 mm were taken in August only, and larger pelagic specimens were taken August through December. Demersal juveniles were taken from a single October collection.

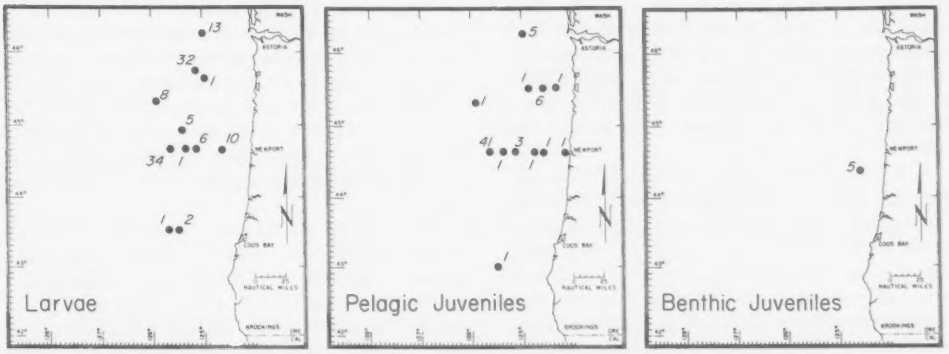

FIGURE 9.—Number of specimens and location of capture of larvae and juveniles of *Sebastes zacentrus* off Oregon (1961-78) described in this paper.

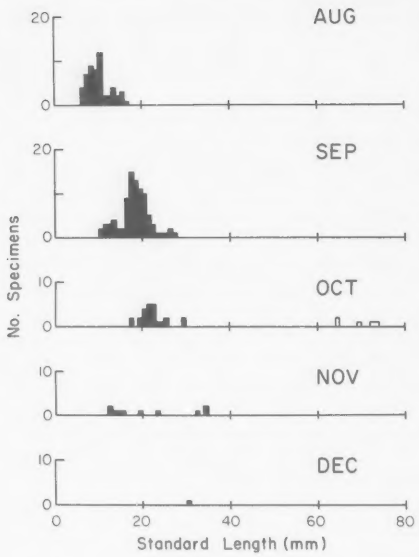

FIGURE 10.—Seasonal occurrence of larvae and juveniles of *Sebastes zacentrus* off Oregon. Data from 1961 through 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

COMPARISONS

Prior to this paper, developmental series of 12 of the 69 northeast Pacific (including Gulf of California) species of *Sebastes* had been described: *S. cortezi*, *S. crameri*, *S.* Gulf Type A, *S. flavidus*, *S. helvomaculatus*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanops*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger* (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980). Comparisons among a number of these species were discussed by Richardson and Laroche (1979) and Laroche and Richardson (1980).

Young stages of *S. entomelas* are relatively slender, with relatively light pigmentation, only moderate head spines, and pectoral and pelvic fins of moderate length. The ontogeny of *S. entomelas* is very similar to that of *S. flavidus* and *S. melanops* which also are moderately slender with only moderate head spines. Pigmentation develops in similar fashion in all three species, i.e., along the dorsal and lateral midlines, although it is less intense in *S. entomelas*. None of the three species develop pigment saddles. Larvae and juveniles of the three are separable by meristic characters.

Young *S. zacentrus* are comparatively deep bodied, with relatively large head and head spines, rather light pigmentation, moderately long pectoral fins, and relatively long pelvic fins especially in the early stages. Other deep-bodied (>30% SL) forms include *S. crameri*, *S. melanostomus*, and *S. pinniger*. Among these species, head spines are pronounced in all but *S. crameri*. The early lack of pigmentation and later development of five pigment saddles in *S. zacentrus* is shared with *S. crameri*, *S. helvomaculatus*, *S. levis*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger*, although the saddles of *S. zacentrus* are less distinct than in the other species. The presence of pigment along the dorsal body surface beneath the dorsal fins of postflexion larvae and pelagic juveniles of *S. zacentrus* is also seen in *S. flavidus*, *S. jordani*, and *S. melanops*. These three species develop a dense dorsolateral covering of melanophores that is not restricted to saddles. Larvae and juveniles of *S. zacentrus* are distinguishable from all of these species on the basis of meristic characters.

HEAD SPINE NOTES

A group of four similar species, *S. entomelas*, *S. flavidus*, *S. melanops*, and *S. mystinus* occur off Oregon and are difficult to identify and separate as larvae and juveniles. We have discovered that literature describing head spine patterns among this group of species is inaccurate and contradictory. After completion of our work on *S. flavidus* and *S. melanops* (Laroche and Richardson 1980) and during the course of our present work on *S. entomelas*, we found undescribed variation in head spine patterns among the species of this group. To insure accurate identification of variant specimens, we quantified and compiled data on spine pattern variation among this group of species. This new information is summarized here. It will aid in identification and separation of the species within the group, particularly of variant specimens.

The original description of *Sebastes entomelas* (Jordan and Gilbert 1880) described the preocular, supraocular, and postocular spines as minute, sharp, and concealed by scales. Phillips (1957) reported the above spines plus the tympanic spine were present on specimens "under about eight inches ..." (203 mm) long and become "nearly all obsolete" in large specimens with occasionally the

tips of the preocular spine weakly present. Hitz (1965) indicated that only the preocular spine is present. Hart (1973) stated that head spines are absent or weakly present, represented by the tip of the preocular spine. The original description of *S. mystinus* (Jordan and Gilbert 1881) stated that the "top of head" is without spines, with the exception of a very small nasal spine and sometimes a preocular spine present. Phillips (1957) and Hitz (1965) also reported this spine pattern. Miller and Lea's (1972) key to the rockfishes of California placed *S. mystinus* in the category of having head spines "weak or obsolete." Hart (1973) reported nasal and "... occasionally minute preopercular [sic = preocular] spines present" with other spines usually obsolete.

Supraorbital spines are small even in juveniles and have often been overlooked on *S. entomelas* and *S. mystinus*. We found that preocular, supraocular, postocular, and tympanic spines are usually present in both *S. entomelas* and *S. mystinus*, although the first two spines may be absent on one side of the head. The only exception observed was one juvenile *S. mystinus* which lacked both preocular spines. These spines eventually become overgrown by scales, tissue, and bone but using a dissecting microscope they are visible on all specimens examined including adults to 342 mm. However, scales and tissue must first be probed away before observation in *S. mystinus* >150 mm. In *S. entomelas* (115 pelagic juveniles, 49-78 mm) from Oregon, 4% lacked one preocular spine and 4% lacked one supraocular spine. In *S. mystinus* (135 pelagic juveniles, 51-71 mm) from Oregon, 6% lacked one preocular spine, and no specimen lacked a supraocular spine.

During our previous study of *S. flavidus* and *S. melanops* (Laroche and Richardson 1980) some variation in supraorbital head spine patterns (i.e., occasional presence of preocular and supraocular spines) was observed which could potentially cause confusion with *S. entomelas*. Although similar, *S. mystinus* has distinctive fin and scale counts (Laroche and Richardson 1980). Because we lacked material to quantify the spine variations, we excluded any variants (i.e., any specimens having preocular or supraocular spines) from the *S. flavidus* and *S. melanops* selected for the developmental series to insure positive identification. New data quantifying spine pattern variation in juveniles of these two species are presented here (Table 8). Presence of a preocular spine is quite rare but occurrence of a supraocular spine is more variable particularly in specimens from Oregon. Separation of *S. entomelas* from these two species is still possible for most specimens based on presence or absence of the preocular spine since >96% of *S. entomelas* and <2% of *S. flavidus* and *S. melanops* have one. Scale and fin ray counts further distinguish these species as described by Laroche and Richardson (1980).

ACKNOWLEDGMENTS

We wish to thank the following people for providing specimens for examination: William Barss, Carl Bond, Tina Eschevera, William Eschmeyer, Wendy Gabriel, Gary Hettman, Michael Hosie, Howard Jones, Earl Krygier, Robert Lea, Jerry Lucas, Lawrence Moulton, William Pearcy, and Jose Sepulveda-Vidal. Special thanks are extended to William G. Pearcy for allowing us to use his extensive midwater trawl collections from waters off Oregon and to Joan Newman for typing the tables and somehow maintaining good humor.

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TABLE 8.—Percentage occurrence of preocular and supraocular spines in juvenile *Sebastes flavidus* and *S. melanops*.

Species	Preocular spines			Supraocular spines		
	Absent both sides	Absent one side	Present both sides	Absent both sides	Absent one side	Present both sides
S. flavidus:						
[1]British Columbia (*N* = 37;42-56 mm)	100	0	0	95	5	0
[2]Oregon (offshore) (*N* = 72;47-59 mm)	98	2	0	64	28	8
S. melanops:						
[1]British Columbia (*N* = 98;45-66 mm)	100	0	0	96	4	0
[2]Oregon (offshore) (*N* = 105;43-60 mm)	98	1	1	51	30	18
[1]Oregon (tidepools) (*N* = 101;43-60 mm)	100	0	0	69	23	8
[1]California (tidepools) (*N* = 80;41-53 mm)	80	0	0	70	9	1

[1]Benthic juveniles.
[2]Pelagic juveniles.

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APPENDIX TABLE 1.— Frequency distributions of soft fin rays, lateral line pores, diagonal scale rows below the lateral line, and gill rakers for juvenile and adult *Sebastes emphaeus*, *S. proriger*, *S. wilsoni*, and *S. zacentrus*.

Species	Side	Pectoral fin rays			Dorsal fin soft rays				Anal fin soft rays			Lateral line pores																		
		16	17	18	13	14	15	16	6	7	8	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	*N*	$\bar{x}$	SD
S. emphaeus[1]	Left	—	35	2	2	33	2	—	—	35	2	—	—	1	7	5	10	5	3	4	1	1	—	—	—	—	—	—	37	42.3	1.9
	Right	—	35	2								—	—	1	5	7	7	8	4	3	2	—	—	—	—	—	—	—	37	42.4	1.8
S. proriger[2]	Left	3	44	—	1	22	22	1	2	44	—	—	—	—	—	—	—	—	1	—	—	—	9	8	6	10	8	5	47	50.2	1.9
	Right	—	46	1								—	—	—	—	—	—	—	—	—	1	6	5	9	10	8	2	6	47	49.8	1.9
S. wilsoni[3]	Left	1	18	—	2	15	2	—	17	2	—	1	—	—	3	4	5	3	3	—	—	1	—	—	—	—	—	—	20	42.0	2.1
	Right	1	18	—								1	—	—	7	1	3	3	3	1	—	—	—	—	—	—	—	—	19	41.6	2.0
S. zacentrus[4]	Left	2	36	2	5	30	4	1	3	37	—	—	3	2	8	8	3	6	7	1	1	1	—	1	—	—	—	—	40	41.8	2.2
	Right	2	35	3								—	1	1	8	8	7	6	4	2	—	1	1	—	1	—	—	—	40	42.2	2.4

Species	Side	Diagonal scale rows below lateral line																								
		41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	*N*	$\bar{x}$	SD
S. emphaeus	Left	1	2	2	9	8	8	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	37	45.0	1.6
	Right	—	—	2	4	6	13	4	3	1	1	—	—	—	—	—	—	—	—	—	—	—	34	45.9	1.6
S. proriger	Left	—	—	—	—	—	—	—	—	—	—	—	—	1	4	5	5	4	2	1	—	1	23	56.0	1.9
	Right	—	—	—	—	—	—	—	—	—	1	—	—	1	3	2	4	2	3	3	1	1	21	56.4	2.6
S. wilsoni	Left	—	—	1	1	1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	7	46.0	2.2
	Right	—	—	—	2	1	—	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	6	46.0	2.3
S. zacentrus	Left	—	—	—	—	4	4	2	4	5	3	1	—	—	1	—	—	—	—	—	—	—	24	47.9	2.2
	Right	—	—	1	1	4	4	3	2	5	3	—	—	1	1	—	—	—	—	—	—	—	25	47.6	2.7

Species	Side	Gill rakers on lower bar of 1st gill arch									Gill rakers on upper bar of 1st gill arch					Total gill rakers on 1st gill arch														
		23	24	25	26	27	28	29	30	31	9	10	11	12	13	32	33	34	35	36	37	38	39	40	41	42	43	*N*	$\bar{x}$	SD
S. emphaeus	Left	—	—	—	—	—	5	13	15	4	—	—	17	17	2	—	—	—	—	—	—	—	4	6	12	11	3	36	41.1	1.1
	Right	—	—	—	—	—	5	7	22	3	—	—	18	16	3	—	—	—	—	—	—	—	4	3	14	13	3	37	41.2	1.1
S. proriger	Left	—	—	—	11	17	18	1	—	—	—	7	32	8	—	—	—	—	—	1	11	18	12	4	1	1	—	48	38.3	1.2
	Right	—	—	—	8	23	12	2	1	—	—	9	35	2	—	—	—	—	—	2	11	18	13	1	—	—	—	45	38.0	0.9
S. wilsoni	Left	—	—	—	—	2	9	8	1	—	—	18	2	—	—	—	—	—	—	—	—	2	8	8	2	—	—	20	39.5	0.8
	Right	—	—	—	—	1	10	7	2	—	—	16	4	—	—	—	—	—	—	—	—	1	10	4	4	1	—	20	39.7	1.0
S. zacentrus	Left	1	7	17	14	1	—	—	—	—	1	34	5	—	—	1	—	6	18	10	5	—	—	—	—	—	—	40	35.3	1.0
	Right	1	3	17	18	1	—	—	—	—	3	34	3	—	—	1	—	4	16	16	3	—	—	—	—	—	—	40	35.4	1.0

[1]Thirty-five *S. emphaeus* collected at lat. 40°12.9′ N, long. 124°23.7′ W off northern California, and two specimens were collected from Hein Bank (lat. 48°21.5′ N, long. 123°02.5′ W).
[2]All *S. proriger* were collected off Oregon between lat. 43°59′ and 45°09′ N.
[3]*Sebastes wilsoni* were collected off Oregon and California between lat. 36°52′ and 45°56′ N.
[4]All *S. zacentrus* were collected off Oregon between lat. 43°23.7′ and 45°09′ N.

CONTRIBUTION TO THE LIFE HISTORY OF THE DEEP-SEA KING CRAB, *LITHODES COUESI*, IN THE GULF OF ALASKA[1]

DAVID A. SOMERTON[2]

ABSTRACT

Lithodes couesi is a deepwater relative of the commercially important Alaskan king crabs, *Paralithodes camtschatica*, *P. platypus*, and *L. aequispina*. Compared with the *Paralithodes* species, which are primarily restricted to the continental shelf, *L. couesi* displays a variety of features which appear to be adaptations for life in deeper water on the continental slope, including elongated legs, red coloration, inflated branchial chambers, asynchronous spawning, and large eggs. Fecundity of *L. couesi* increases asymptotically with carapace length according to the relationship $E = 4{,}329 - 3.19 \times 10^9 e^{-0.172L}$. The size of 50% maturity is reached at 91.4 mm for males and at 80.2 mm for females.

The deep-sea king crab, *Lithodes couesi*, is a little known relative of the three species of king crab, *Paralithodes camtschatica*, *P. platypus*, and *L. aequispina*, commercially harvested in Alaska. Since its original description (Benedict 1895), *L. couesi* has been discussed only in taxonomic works (Rathbun 1904; Schmitt 1921; Makarov 1938; Sakai 1971); other than its geographical distribution (San Diego, Calif., to Onohama, Japan) and depths of occurrence (542-1,125 m), nothing has been reported concerning the life history of this species.

Considering its rather large size and conspicuous bright red color, it is surprising that *L. couesi* has not received more attention. One reason for this is that benthic sampling surveys infrequently reach the depths inhabited by *L. couesi*, and those that do typically are not designed to catch a large number of specimens. However, in 1979 a National Marine Fisheries Service (NMFS) cruise surveying the commercial fishing potential of seamounts in the Gulf of Alaska caught nearly 1,500 *L. couesi* in large baited traps. The present study is based on these specimens.

Although *L. couesi* is unlikely soon to become the target of a commercial fishery due to the great depths it inhabits, the high value of crab and the fluctuating supply of other Alaskan crab species may stimulate technological developments making deepwater crab fishing more economical. Such developments have already occurred in the fishery for another deepwater crab, *Geryon quinquedens*, along the east coast of North America (Wigley et al. 1975). This paper is intended to provide a comparison of life history characteristics between *L. couesi* and shallow-water king crabs, as well as to provide some information needed by fisheries managers in the event *L. couesi* were to become commercially important.

METHODS

Samples of *L. couesi* were collected between 31 May and 5 July 1979 on an NMFS stock assessment cruise to eight seamounts located in the central Gulf of Alaska (Figure 1). All specimens except three were captured in baited traps. Three types of trap were used: rectangular sablefish, *Anoplopoma fimbria*, traps measuring 0.8 m × 0.8 m × 2.5 m and covered with 8.9 cm (bar measure) webbing; conical sablefish traps measuring 0.7 m high × 1.2 m base diameter × 0.9 m top diameter and covered with 7.5 cm webbing; and rectangular king crab traps measuring 1.8 m × 1.8 m × 0.6 m and covered with 11.4 cm webbing. Traps were arranged at 91.5 m intervals along a 1,006.5 m groundline having surface floats connected to both ends. A typical set of gear included four or five of each type of sablefish traps, plus two king crab traps in 8 of the 25 sets. A total of 232 traps (102 conical, 114 rectangular, 16 king crab) were set. Three small specimens of *L. couesi* were obtained in one haul of a bottom trawl.

All seamounts were extremely steep sided, rising approximately 3,000 m from the seafloor to relatively flat summits composed of rock outcrops

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Manuscript accepted October 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

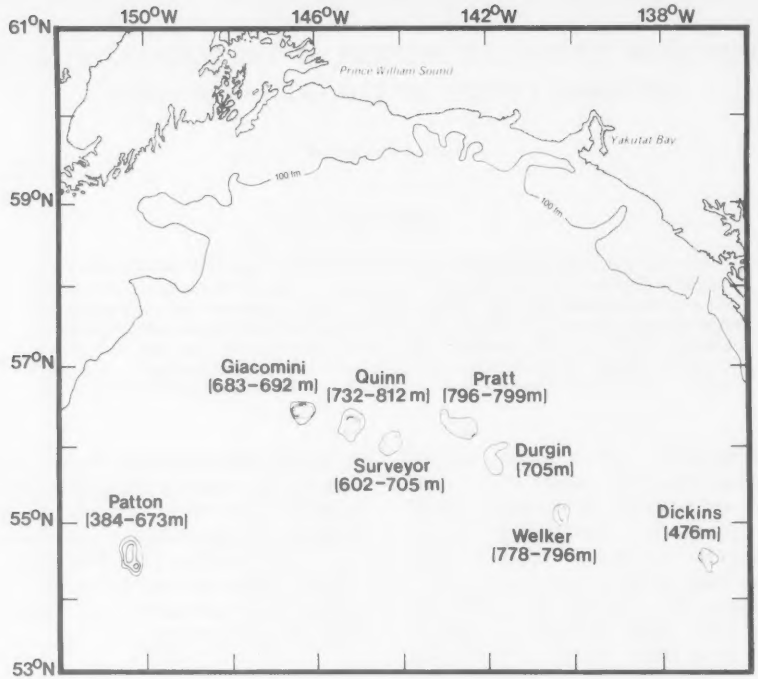

FIGURE 1.—Location of the eight seamounts which were surveyed on a 1979 NMFS cruise to the Gulf of Alaska. The range of sampling depths on each seamount is indicated.

with intervening sediments. This physiography limited sampling to the seamount tops. Sampling depths ranged from 384 m on the Patton Seamount to 850 m on the Quinn Seamount.

The carapace lengths of all crabs and the right chela heights of males were measured to the nearest 0.1 mm using vernier calipers (see Wallace et al. (1949) for a description of these two measurements). The reproductive condition of females was scored according to the following six-point scale:

1) Immature—white undeveloped ovaries and no egg remnants on the pleopod bristles.
2) Virgin—orange developed ovaries and no egg remnants on the pleopod bristles.
3) New eggs—orange external eggs with no evidence of embryonic eyes.
4) Developing eggs—tan external eggs with obvious dark embryonic eyes.
5) Hatching eggs—partial clutch of well-developed eggs, with remnants of hatched eggs attached to pleopod bristles and occasionally with prezoea on the egg mass.
6) Completely hatched—no external eggs, but remnants of eggs, especially the egg funiculi, attached to the pleopod bristles.

Abdomens, complete with attached eggs, were removed from a selected number of females and preserved in buffered 10% Formalin.[3] In the laboratory, the pleopods from females with new and developing eggs were removed and dried. After freeing the eggs from the pleopods, the total clutch was weighed and a subsample was weighed and counted. Total egg number was calculated by dividing total clutch weight by the average egg weight of the subsample. Maximum egg length was measured to 0.1 mm using an ocular micrometer. Measured eggs were well developed and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

apparently close to hatching, and had been stored in 33% isopropyl alcohol after being fixed in Formalin.

RESULTS AND DISCUSSION

Depth Distribution

Specimens of *L. couesi* were collected in every trap set from the shallowest in 384 m to the deepest in 850 m. Four sets on two seamounts were at depths less than the depth range (542-1,125 m) previously recorded for this species (Sakai 1971).

Lithodes couesi occurs shallower on seamounts than on the continental slope. This hypothesis is supported by the results of a concurrent NMFS survey of the southeast Alaska continental slope that sampled roughly the same latitudes (54°-58° N) and depths (237-711 m) and used the same types of traps as the seamount study. Although depths <550 m were thoroughly sampled, specimens of *L. couesi* were not taken in <592 m (H. Zenger[4]).

The shallow distribution of *L. couesi* on seamounts may be due to the absence of a predator or competitor which is able to exclude it from similar depths along the continental slope. Because seamounts are isolated from the ocean surface and from coastal areas, they are essentially submarine islands inhabited only by species that are able to tolerate the available depth range and that possess sufficient dispersal capabilities to reach seamounts from the continental slope. If a predator or competitor were unable to colonize the seamounts, *L. couesi* may respond by expanding its range into shallower water. A similar pattern of competitive release and altitudinal expansion has been reported for birds on South Pacific islands (Diamond 1975).

Size Distribution

The size distribution of each sex was nearly unimodal with a mode at about 108 mm for males and 92 mm for females (Figure 2). The lack of an appreciable number of crabs <70 mm is probably due to size selectivity of the sampling gear, rather than a lack of small crabs on the seamount tops, because three of the four smallest specimens were caught with a bottom trawl in an area of the Patton Seamount where only larger crabs were obtained with traps.

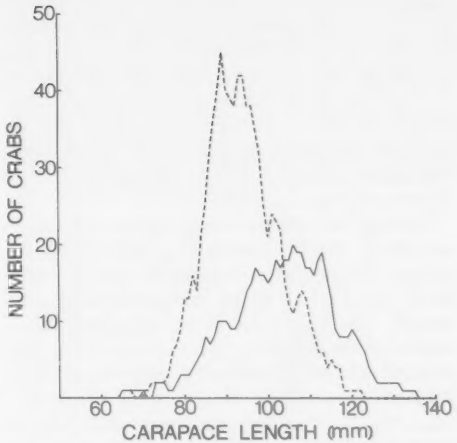

FIGURE 2.—Size distribution of male (solid line) and female (dotted line) *Lithodes couesi* by 2 mm size intervals from trap samples from Gulf of Alaska seamounts.

Other species of king crabs, especially *P. camtschatica* and *P. platypus*, display size stratification with depth; adults generally occur deeper than juveniles (pers. obs.). To determine if *L. couesi* also stratify, crab size was regressed against depth. Only the sizes of crabs from sablefish traps were used in the regression because king crab traps caught significantly larger crabs than sablefish traps when both types were fished together (t-test, $P<0.001$) and because king crab traps were not used on every seamount. For males, the slope of the regression line was not significant ($P = 0.289$). For females, the slope was significant ($P = 0.030$) and negative, indicating that larger females occur in shallow water. However, there was little variation in sampling depth on each seamount; thus, size variation with depth cannot be separated from size variation between seamounts.

Sex Ratio

In total, 880 females and 577 males were captured in 24 trap sets. The large preponderance of females suggested that the sex ratio may not be 1:1. If the sex of each specimen were independent of the sex of other specimens in the same set, then the observed proportion male, 0.40, is signifi-

[4]H. Zenger, Fishery Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, pers. commun. June 1980.

cantly different than 0.50 ($Z = 7.8$, $P \leq 0.001$). Sex ratio, however, was not homogenous between trap sets ($\chi^2 = 137.5$, $P \leq 0.0001$), indicating that the sex of each specimen was not independent of other specimens but highly correlated. Thus, females tended to be caught with other females and males tended to be caught with other males. Segregation by sex is also commonly observed for *P. camtschatica* (pers. obs.).

Although the sexes of crabs within each set are correlated, the hypothesis of a 0.50 proportion male in the population can still be tested if each set is assumed to be an independent random sample. The test is made by calculating a *t*-statistic from the mean and variance of the proportion male within individual trap sets. Because the number of crabs within each set varied considerably, the mean proportion was calculated as a weighted average, with the weighting factors equal to the number of crabs in each set (Cochran 1943). The *t*-test was not significant ($t = 0.396$, $P = 0.86$); thus, a 1:1 sex ratio is not rejected.

Female Reproductive Condition

The number of female *L. couesi* in each of the six categories of reproductive condition is shown as a function of size in Figure 3. Eighty-six percent of the females examined were mature (categories 3-6). Virgin females had partially developed ovaries and appeared to have never spawned previously. Assuming virgin female *L. couesi* require the same length of time to complete maturity as "pubescent" female *P. camtschatica* (Powell et al. 1973), their first spawning will occur soon after their next molt in the following spring.

Mature female *L. couesi* display more heterogeneity in their reproductive condition than female *P. camtschatica*. This is exemplified in the following table, where the percentage of mature female *L. couesi* in each of the four mature reproductive categories is compared with the equivalent reproductive categories of female *P. camtschatica* collected in the eastern Bering Sea at the same time as the seamount survey.

Species	New eggs	Developing eggs	Hatching eggs	Completely hatched eggs
L. couesi	50	35	6	9
P. camtschatica	97	..... 2		1

Although no distinction was made between developing and hatching eggs for *P. camtschatica*, it is evident that *P. camtschatica* had nearly completed spawning and were carrying new eggs, whereas *L. couesi* had not completed spawning and were carrying eggs in a variety of developmental stages.

If *L. couesi* are similar to *P. camtschatica* in spawning soon after hatching the previous clutch, then the heterogeneity in their reproductive condition can be interpreted in either of two ways. First, *L. couesi* were sampled midway in their spawning season; therefore, the maturing eggs hatch later in the season. Second, *L. couesi* were sampled at the end of the spawning season; therefore, the maturing eggs are from spawning in the current season and hatch in the succeeding year. The difference in these interpretations

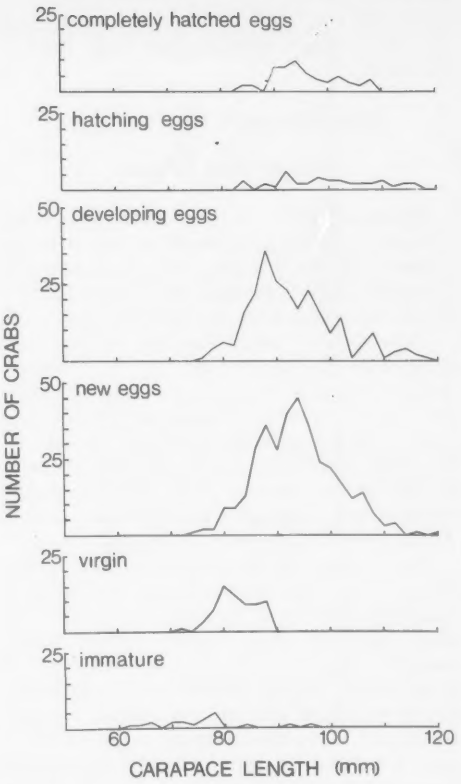

FIGURE 3.—Number of female *Lithodes couesi* by 2 mm size intervals in each of the six categories of reproductive condition described in the text.

reflects the degree of reproductive synchrony in the population. If the first interpretation were correct, *L. couesi* could be as synchronized as *P. camtschatica* and the heterogeneity in reproductive condition could merely be due to fortuitous timing of the survey. But if the second interpretation were correct, *L. couesi* would be quite asynchronous compared with *P. camtschatica* because, at least in *P. camtschatica*, the eyed (developing) eyes would have been spawned at least 4 mo previous to sampling (G. C. Powell[5]). Although the embryological development of *L. couesi* eggs was not studied—this would be necessary to completely resolve the question—I believe that the second interpretation, that *L. couesi* has an asynchronous spawning, is correct because the eggs classified as developing were clearly in a much earlier stage of development than were the hatching eggs.

The asynchronous spawning of *L. couesi* is probably related to the great depths which it inhabits. Temperate species having planktotrophic larvae typically have synchronous breeding cycles because of the rather brief periods which are optimum for larval survival. Since seasonal fluctuations are damped with depth, *L. couesi* may be unable to detect seasonal cues with precision, or more likely, may have larvae which do not rise to the euphotic zone and do not need to be synchronized with the surface production cycle. Asynchronous spawning was also observed for another deepwater crab, *Geryon quinquedens* (Haefner 1978). Crustaceans living at depths greater than *L. couesi* have such asynchrony in spawning that seasonal peaks in spawning activity are absent (Rokop 1977).

Size of Maturity

Maturity of females was determined by the presence of eggs or egg remnants on the pleopods. Thus, reproductive categories 1 and 2 were considered immature and categories 3 to 6 were considered mature. Maturity of males was determined from the size of the chela relative to the size of the carapace using a method discussed in Somerton (1980). This method assumes that when chela and carapace measurements are plotted against each other on a double logarithmic scale, the points lie along two straight lines, one describing the relative growth for juveniles, the other describing the relative growth for adults. A computer technique was used to iteratively fit two lines to the data until the best fit (minimal residual sum of squares) was achieved (Figure 4). Maturity was then based on the final assignment to one of the two categories.

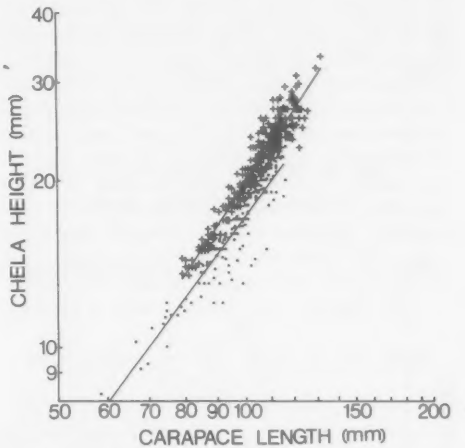

FIGURE 4.—Classification of male *Lithodes couesi* chela height and carapace length measurements into juvenile (dots) and adult (pluses) categories. The relative growth of the chela is described for juveniles by the lower line (CH = 1.52 CL − 4.17; SD for intercept and slope are 0.19 and 0.04) and for adults by the upper line (CH = 1.70 CL − 4.83; SD for intercept and slope are 0.13 and 0.03). Regression methods of Somerton (1980), see text.

The size of 50% maturity was estimated by fitting a logistic equation to the percentage mature by size using the methods discussed in Somerton (1980), then evaluating the fitted equation to determine the size corresponding to 50% mature. Percentage mature and the fitted logistic equation are shown for both sexes in Figure 5. Estimated sizes of 50% maturity were 91.4 mm for males and 80.2 mm for females.

Fecundity

Fecundity of *L. couesi* increases up to a size of 95 mm and remains fairly constant thereafter (Figure 6). The apparent curvilinear relationship between fecundity and size is similar to that reported for *P. platypus* (Sasakawa 1975) but unlike the strict linear relationships reported for

[5]G. C. Powell, Fishery Biologist, Alaska Department of Fish and Game, Division of Commercial Fisheries, P.O. Box 686, Kodiak, AK 99615, pers. commun. June 1980.

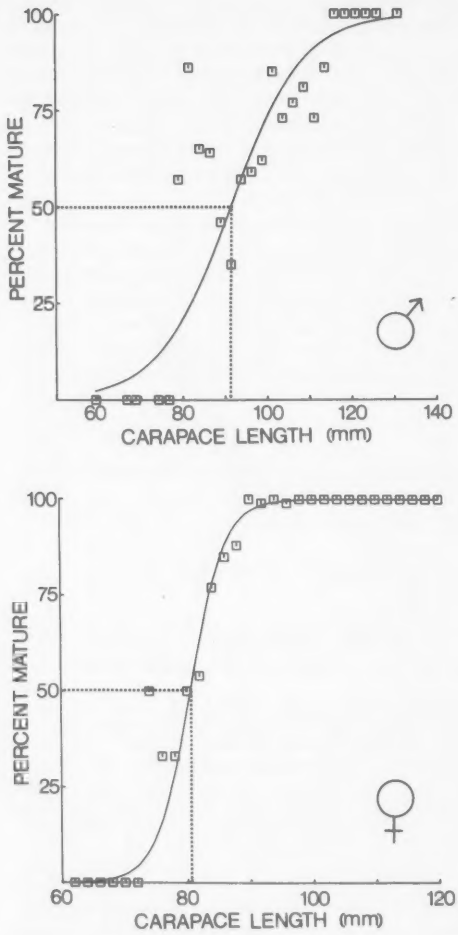

FIGURE 5.—Percentage of male (upper) and female (lower) *Lithodes couesi* classified adult as a function of size. The size of 50% maturity was estimated by first fitting a logistic equation to the data, then determining the size (shown by dotted lines) corresponding to 50% mature.

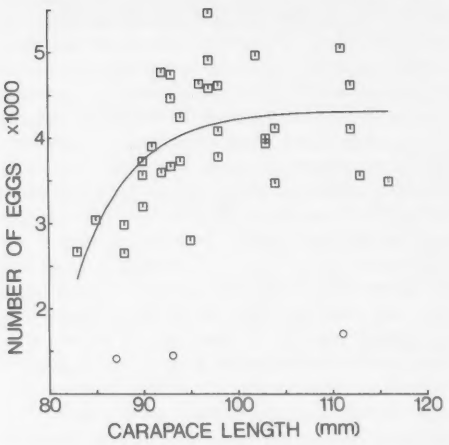

FIGURE 6.—Fecundity of *Lithodes couesi* as a function of size. An asymptotic curve was fit to the data using methods described in the text. Three specimens (shown by circles) had conspicuously fewer eggs. Although these females did not appear to be damaged, their fecundities were excluded from the analysis.

P. camtschatica (Haynes 1968), *L. aequispina* (Hiramoto and Sato 1970), and *L. antarctica* (Guzman and Campodonico 1972).

An attempt was made to develop an appropriate functional relationship to describe the fecundity and size of *L. couesi*. To determine whether or not this relationship should be curvilinear, the fit of a second degree polynomial was statistically compared with that of a straight line. The coefficient of the squared term of the polynomial was highly significant ($F = 12.23$, $P < 0.001$), indicating that the polynomial fit the data better than a straight line; however, a second degree polynomial was not a good relationship because the predicted fecundity did not increase monotonically with size. Since it is unlikely that fecundity reaches some maximum and then diminishes with size, an asymptotic curvilinear relationship was considered. The chosen equation is $E = E_\infty - Ae^{-BL}$, where E is egg number, L is carapace length, E_∞ is a parameter representing the theoretical maximum number of eggs that can be carried, and A and B are parameters controlling the rate at which the maximum egg number is achieved. Using nonlinear regression, the best fit was obtained when $E = 4{,}329 - 3.19 \times 10^9 \, e^{-0.172L}$ (Figure 6).

If the number of eggs a female could carry were limited either by the length of the pleopods or by the volume of the brood chamber enclosed between the abdomen and the sternum, then fecundity should increase in proportion to the carapace length raised to a power of one or greater, that is, fecundity should be an upwards concave function of size. The best fitting equation is concave downwards, which indicates that some other mechanism limits fecundity in *L. couesi*. One possible explanation is that the low oxygen con-

centrations at the depth inhabited by *L. couesi* reduce the ability of females to aerate clutches larger than some fixed size.

One consequence of an asymptotic form to the fecundity and size relationship is that the reproductive effort, or the proportion of the total energy intake devoted to reproduction, must decrease over some part of the reproductive lifespan of *L. couesi*. Theory predicts and many animals display an increase in reproductive effort with age (Pianka and Parker 1975). Since fecundity appears to be fairly constant over approximately one-half of the mature size range of *L. couesi*, reproductive effort could increase only if either egg size increased with age or growth ceased. Individual dried egg weight, however, does not increase with crab size ($P = 0.15$), and the lack of wear and accumulation of epifauna on the exoskeleton suggests that molting, and presumably growth, continues throughout the life of females.

Egg Size

Lithodes couesi eggs in a late stage of development have a mean length of 2.3 mm (SD = 0.076, $N = 33$). This size is quite similar to previous estimates of mean or median egg size reported for other species in the genus *Lithodes*—*L. antarctica*, 2.2 mm (Guzman and Campodonico 1972); *L. aequispina*, 2.1 mm (Hiramoto and Sato 1970)—but roughly twice the egg size reported for species in the genus *Paralithodes*—*P. camtschatica*, 1.0 mm (Haynes 1968); *P. platypus*, 1.2 mm (Sasakawa 1975).

The larger size of *Lithodes* spp. eggs compared with *Paralithodes* spp. eggs conforms to a theory of egg size and pattern of larvae development first discussed by Thorson (1950), which proposes that benthic invertebrates generally have large eggs and lecithotrophic larvae in high latitudes or in deep water, but have small eggs and planktotrophic larvae in other areas. At great depths or at high latitudes water temperatures are low and larval development is protracted. Species may compensate for slow larval development by producing larger and more yolky eggs, which in turn result in larger larvae with greater energy reserves. These larval features may be necessary to allow the larvae either to migrate to the surface, to capture a broader array of food items, or to forgo feeding entirely. Stage 1 zoeae of *L. couesi* have conspicuously more yolk than *P. camtschatica* larvae in the same stage of development (J. Bowerman[6]), but it is unclear whether or not these larvae migrate to the surface. Unusually large eggs have been previously reported for abyssal shrimp (Zarenkov 1965) and abyssal crabs (Garth and Haig 1971).

Parasites

Of the 674 female *L. couesi* examined, 5 were parasitized by the rhizocephalan, *Briarosaccus callosus*. All five females were >90 mm and, on the basis of size alone, should have been mature, but none were carrying eggs and all had unusually small pleopods compared with uninfected crabs of similar size. Thus, similar to other species of crabs (Barnes 1974), *L. couesi* females are apparently castrated by *B. callosus*. One male *L. couesi* was also observed with the parasite; however, the abdomens of males were not routinely examined and other parasitized males could have been missed. *Briarosaccus callosus* has been previously reported as a parasite of *L. couesi* (Boschma 1970).

Adaptations for Life on the Upper Slope

Lithodes couesi is conspicuously different in appearance (Figure 7) from the shallow-water king crabs, *P. camtschatica* and *P. platypus*, because of three features: 1) bright red, 2) inflated branchial chambers, 3) elongated legs. All of these features are apparently adaptations for living in deeper water.

The red coloration of deepwater crustaceans has long been a subject for speculation, but the general consensus is that within some range of depth, red is cryptic due to the rapid attenuation of red light originating from the surface and the low in situ production of red light from bioluminescence (Marshall 1954). At depths greater than this range, the ambient light is too weak for visual predators and crustaceans are often white or transparent (Zenkevich and Birstein 1956); at depths shallower than this range, red may be too conspicuous to visual predators and the red cartenoid pigments are often complexed with proteins to produce blue, green, and brown pigments (Goodwin 1960).

Crabs living on the continental slope have branchial chambers which are more inflated than

[6]J. Bowerman, Fishery Biologist, Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615, pers. commun. June 1980.

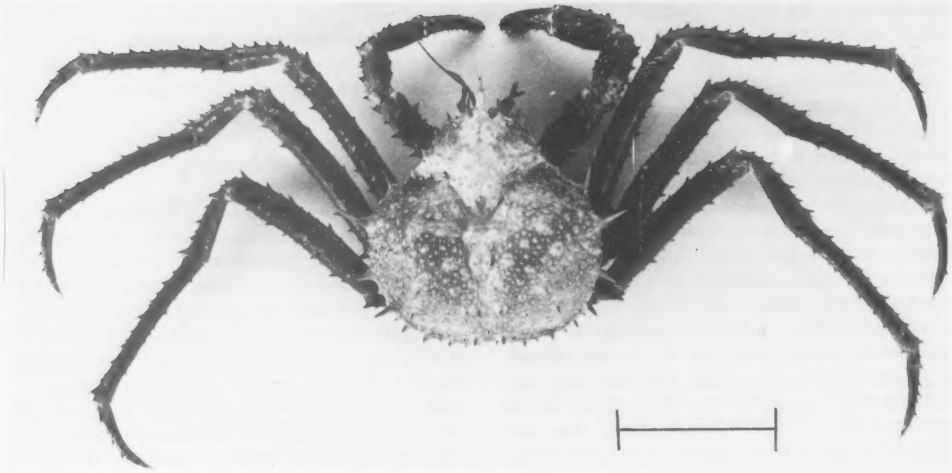

FIGURE 7.—A male specimen of *Lithodes couesi* (a 100 mm bar is included for scale). Generally, *L. couesi* are bright red with the carapace being somewhat lighter than the legs; however, occasional specimens will be light pink. Great variability was found in the length of the spines along the lateral margins of the carapace. The above specimen has especially long spines.

those of crabs living on the shelf. The degree of branchial inflation was quantified by Takeshita et al. (1978) for three anomuran crabs in the family Lithodidae—*P. camtschatica*, *L. aequispina*, *Paralomis verrilli*—and four brachyuran crabs in the genus *Chionoecetes*—*C. bairdi*, *C. opilio*, *C. japonicus*, *C. tanneri*—using moire photography. For both the anomuran and brachyuran crabs, the branchial chambers were more inflated in the species living at greater depths. In the present study, a similar type of assessment was not made for *L. couesi* due to a lack of suitable photographic equipment; however, the inflation of the branchial chambers appears to be greater than *L. aequispina* (a shallower species) and less than *P. verrilli* (a deeper species). Although I lack data to demonstrate that enlarged gills are associated with inflated branchial chambers, Rathbun (1893), in the original description of *C. tanneri* (a deep species), remarked that "The carapace is much swollen at the branchial regions" compared with *C. opilio* (a shallower species) and that the gills of *C. tanneri* are about two-fifths longer than the gills of an equal-sized specimen of *C. opilio*.

The inflation of crab branchial chambers with increasing depth is related to the distribution of oxygen in the sea. Typically, the concentration of dissolved oxygen decreases with depth until an oxygen minimum zone is reached, then increases thereafter. In the region of the Gulf of Alaska near the major seamounts, a minimum oxygen concentration of 0.5 ml/l, roughly 7% of the surface concentration, occurs at 1,000 m (Favorite et al. 1976). Since the combined depth ranges of the species considered by Takeshita et al. (1978) extend from 1,400 m to the intertidal, the deeper these species occur, the lower the oxygen concentrations they must deal with. Inflated branchial chambers or unusually large gills have been reported for a brachyuran crab, *Lophorochinia parabranchia* (Garth and Haig 1971), and a mysid, *Gnathophausia ingens* (Childress 1971a), both of which are primarily restricted to oxygen minimum zones.

Lithodes couesi has two additional morphological features allowing respiration in low oxygen concentrations: large exhalent openings and large scaphognathites (appendages located in the exhalent openings and used for pumping water over the gills). Enlargement of these features, compared with related shallow-water lithodid crabs, implies that a relatively greater volume of water is pumped over the gills. *Gnathophausia ingens* was also found to have a large ventilation volume compared with related shallow-water species (Childress 1971a).

To demonstrate that walking legs are more elongated for crab species inhabiting greater depths, two leg dimensions, merus length and propodus length, were compared between deep and shallow species (Table 1). Two trends in relative leg dimensions are evident. First, the legs become thinner with depth; that is, merus height to merus length decreases. Second, the distal portion of the legs becomes relatively longer with depth; that is, propodus length to merus length increases.

TABLE 1.—Merus height (MH) and propodus length (PL) of the right first walking leg, expressed as a fraction of merus length (ML), are shown for one adult male specimen of three species in the family Lithodidae and three species in the genus *Chionoecetes*. Under each taxonomic section, species are arranged according to depth, with the shallowest species at the top, except for *C. bairdi* and *C. opilio*, which occur at similar depths.

Species	MH/ML	PL/ML
Anomura:		
Paralithodes platypus	0.286	0.715
Lithodes aequispina	.255	.823
L. couesi	.189	.882
Brachyura:		
Chionoecetes opilio	.222	.578
C. bairdi	.209	.487
C. tanneri	.158	.655

The selective advantage of long slender legs for deepwater crabs is not obvious. Barnes (1974) suggested that: "Many abyssal crabs have long slender legs for crawling about over soft bottoms." Presumably, this means that the propodi and the dactyli are placed flat on the substrate and used, like snowshoes, to spread the body weight more evenly. However, underwater photographs of both *L. couesi* (Figure 8) and *Geryon quinquedens* (see Wigley et al. 1975, fig. 4) show individuals walking over apparently soft bottoms on the tips of the dactyli. An alternative explanation, suggested by Childress (1971b), is that reduced musculature in

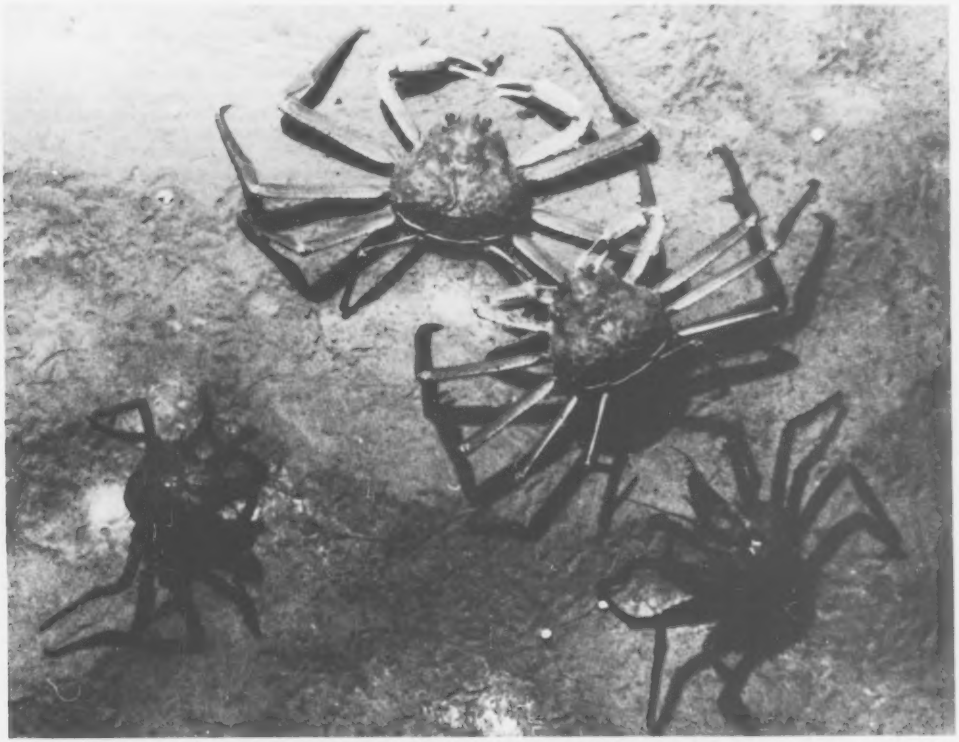

FIGURE 8.—Photograph on the Patton Seamount (500 m) of *Lithodes couesi* (lower) and *Chionoecetes tanneri* (upper) walking across a soft bottom on the tips of their dactyli (photograph taken by P. Raymore).

deepwater crustaceans requires less energy to maintain and thus represents an adaptation for energetic efficiency in a habitat where food is scarce. In addition, long legs may allow a crab to move more rapidly or more economically by taking fewer, larger steps to travel a given distance.

ACKNOWLEDGMENTS

I would like to thank J. N. Cross, C. M. Lynde, R. D. Stevenson, and P. Raymore for reviewing the manuscript and offering helpful suggestions, and J. Orensanz for helping with the field and laboratory work. This research was supported by NORFISH, a marine research project of the University of Washington Sea Grant office and the National Marine Fisheries Service, National Oceanic and Atmospheric Administration, U.S. Department of Commerce.

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THE EFFECT OF THE BOTTOM ON THE FAST START OF FLATFISH *CITHARICHTHYS STIGMAEUS*

P. W. WEBB[1]

ABSTRACT

Fast starts of the speckled sanddab, *Citharichthys stigmaeus*, were initiated by a 1 volt per centimeter direct current electric shock and recorded on movie film at 250 frames per second. Observations on kinematics and performance were made for fast starts of fish accelerating in the water column and from a grid located at a distance of 0, 1, 3, or 6 cm above the true bottom. During acceleration the body was bent into a U-shape relative to the bottom. The body sustained a direct push against the grid when accelerating from that grid. The amplitude of propulsive movements of fish accelerating from the grid was larger than acceleration movements of fish in the water column away from the bottom, because the potential for energy wastage due to recoil of the body was prevented by the grid. The distance between the grid and the bottom had no effect on fast starts, ruling out any hydrodynamic ground effect. Motion of fish accelerating in the water column was continuous and predominantly in the horizontal plane. There was little motion of fish accelerating from the grid until they started pushing against that grid. Motion was predominantly in the vertical plane. The resultant distance traveled by fish accelerating from the grid, measured at the end of the principal acceleration period exceeded that of fish accelerating in the water column. Velocities and acceleration rates were highest for fish accelerating from the grid. It was concluded that contact with the sea bottom would enhance fast-start performance of flatfish.

Fish of the order Pleuronectiformes are unique because the adults lie on one side. The habit of inclining to one side is common among other benthic fish that are normally vertically oriented, but no other group shows the specialized morphological adaptations of flatfish. Various observations on benthic fish suggest that inclining the body or lying on one side is advantageous for camouflage and crypsis (Norman 1966). Large locomotor advantages could also accrue, especially to flatfish orienting their body axis parallel to the ground.

Improvements in locomotor performance of flatfish could occur through two mechanisms: hydrodynamic ground effect and pushing against a rigid substrate. The hydrodynamic ground effect occurs through interaction of the downwash from propulsive surfaces with the ground (i.e., the sea bottom) and increases effective thrust and decreases effective drag (Bramwell 1976; Lighthill 1979). It has been described for birds (Withers and Timko 1977) and for pectoral fin propulsion of the mandarin fish, *Synchropus picturatus* (Blake 1979). Pushing against the substrate is obviously more energy efficient than pushing against water because more muscle power is converted into body motion rather than wasted in accelerating fluid. It is utilized by macrurous decapods (Webb 1979). The relative importance and effectiveness of these mechanisms will depend on how flatfish move their bodies near the ground.

The following experiments were performed to determine if the sea bottom could influence fast-start (acceleration) movements and performance of a typical flatfish. Emphasis was placed on fast starts because of their importance in evasion of predators and in catching elusive prey (Eaton and Bombardieri 1978; Webb and Skadsen 1980).

METHODS

Fish

Speckled sanddab, *Citharichthys stigmaeus* Jordan and Gilbert (family Bothidae) were used. Fish were caught in dip nets by divers along the southern California coast, hence avoiding the damage typical of trawl-caught specimens. Fish were held in a 60,000 l tank at 14° C. They were fed twice a week on frozen brine shrimp.

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Manuscript accepted September 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

Procedures

Individual speckled sanddabs were starved for 24 h. Each fish was lightly anesthetized (MS-222)[2] and a white thread was sewn above the center of mass of the stretched-straight body calculated from previous measurements on a subsample of fish. This reference facilitated later film analysis. Each fish was then placed in an observation arena and allowed to recover for 24 h overnight.

The observation arena consisted of a chamber 45 cm long, 30 cm wide, and 40 cm deep. A fast start is a short duration stereotyped activity during which fish travel short distances but accelerate at high rates to reach large speeds (Eaton et al. 1977; Webb 1978). The size of the arena would not interfere with fast-start activity but would prevent sustained high-speed swimming. This study is concerned only with the former activity.

The observation chamber had a false bottom made from a wire grid (2.5 cm squares made from 0.08 cm diameter wire). A solid bottom was located beneath the grid and could be set 0, 1, 3, or 6 cm beneath. Comparison of performance during fast starts with the grid set at various distances above the solid bottom was expected to show the importance of the hydrodynamic ground effect as differences in performances once physical contact with the grid had ended. Vertical reinforcers prevented the grid from acting as a spring when a force was applied by an accelerating fish. The observation chamber also allowed room for fish to swim in the water column for short distances permitting observation of fast starts in the water column remote from all possible ground interaction.

The bottom was located in one of the four positions beneath the grid while the sanddab became accustomed to the chamber overnight. Next morning a 1.0 V/cm d.c. electric shock was used to initiate a fast start either from the grid or when the sanddab was temporarily stationary in the water column clear of the grid and bottom. All experiments were performed at 14° C.

Fast starts were recorded on movie film at 250 frames/s. A 45° mirror above the observation chamber allowed simultaneous observation of top and bottom views. A floating lid prevented surface ripples distorting the top-view image.

Each fish was killed after an experiment. The body outline was traced on paper. Mass, total length, wetted surface area, location of the center of mass, and muscle mass were measured as described by Webb (1977).

There were no differences in these morphometric characteristics among various groups of speckled sanddabs. Combined values were (mean ±2 SE); mass, 28.96±3.78 g; length, 13.7±0.6 cm; the center of mass, located 5.2±0.2 cm from the nose; wetted surface area, 120±10 cm^2; muscle mass, free of skin and scales, 11.78±2.28 g.

Movie film was analyzed frame by frame to observe kinematics and to measure performance. Details are given by Webb (1978). Briefly, performance was measured for the motion of the center of mass of the stretched-straight body. This point approximates the instantaneous center of mass of the flexing body which is the point about which propulsive forces act. Coordinates for motion of the center of mass were measured in the horizontal and vertical planes. The resultant motion of the center of mass was calculated. Velocities and acceleration rates for these three motions (horizontal, vertical, and resultant) were calculated using moving point linear regression methods. Performance parameters were compared using the *t*-test, and significant differences between means are declared at the 5% level.

RESULTS

Kinematics

There were no differences in kinematics of fish accelerating from the grid set at various distances above the solid bottom. Fast-start kinematics for acceleration from the grids (Figure 1) showed the normal three stages originally described by Weihs (1973). During stage 1, the body was bent into a U-posture (0-80 ms in Figure 1A) comparable to the C-posture of other teleosts when viewed from above (Eaton et al. 1977; Webb 1978). The center of mass showed some recoil (i.e., lateral movement in the opposite direction to the tail, and normal to the fish axis) towards the grid because the fish adopted a posture with the body raised by the median fins before a fast start (Stickney et al. 1973). The body was always bent away from the bottom.

During stage 2 (80-120 ms in Figure 1A), the body was bent in the direction opposite to that of stage 1 as the body curvature traveled caudally along the body. Some point of the body remained in contact with the grid almost to the end of stage 2.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

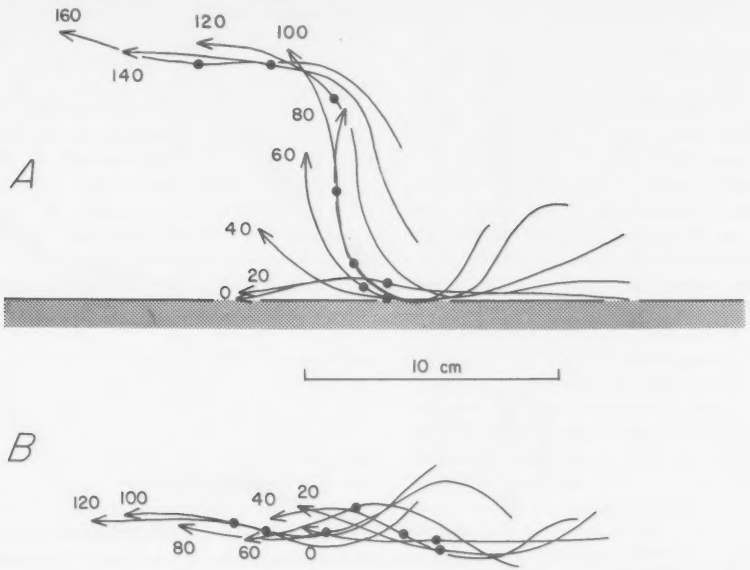

FIGURE 1.—Tracings of the body center-line (seen from the side) at 20 ms intervals to show the acceleration movements during fast starts of *Citharichthys stigmaeus*: A) Acceleration from contact with the grid. B) Acceleration in the water column. Dots show the location of the center of mass of the stretched-straight body. The extended and variable stage 3 following the major acceleration strokes has been omitted for clarity.

The center of mass was propelled vertically away from the ground.

Fast start stage 3, occurring after the major acceleration period, was variable, ranging from an unpowered glide to continued swimming with caudal propagation of propulsive waves sustained from the starting curvature in stage 2.

A typical fast start of a sanddab in the water column away from the bottom is illustrated in Figure 1B. Fast starts in the water column showed the same stages as fast starts from the grid. The amplitude of body movements was usually smaller than those of fish accelerating from the grid. Center of mass recoil, reduced during acceleration from the grid, was observed for fish accelerating in the water column, as seen in other teleosts.

The timing of various fast-start events was similar among groups of fish (Table 1). The duration of stage 1 showed a slight but nonsignificant tendency to decrease as the distance between the grid and the solid bottom increased. The fish accelerating from the grid lost contact after 112 ms, before the completion of stage 2 in 124 ms (Table 1).

Fast-Start Performance

The distance between the solid bottom and the grid had no significant effect on vertical and horizontal distances traveled by the center of mass of speckled sanddabs during fast starts (Figure 2) including distances traveled after losing contact with the grid. This showed that no measurable

TABLE 1.—Results for the duration of fast-start events for *Citharichthys stigmaeus* accelerating from a grid at various distances above a solid bottom and accelerating in the water column. Mean ±2 SE are shown, $n = 10$.

Timing	Acceleration in the water column	Distance between the grid and the solid bottom (cm)				Combined data for acceleration from the grid
		0	1	3	6	
Duration of stage 1, ms	58±8	65±6	65±14	62±8	60±8	63±5
Duration of stages 1 plus 2, ms	105±12	136±18	118±13	149±40	113±9	124±7
Time to end of ground contact, ms	—	116±19	108±9	116±15	113±9	112±6

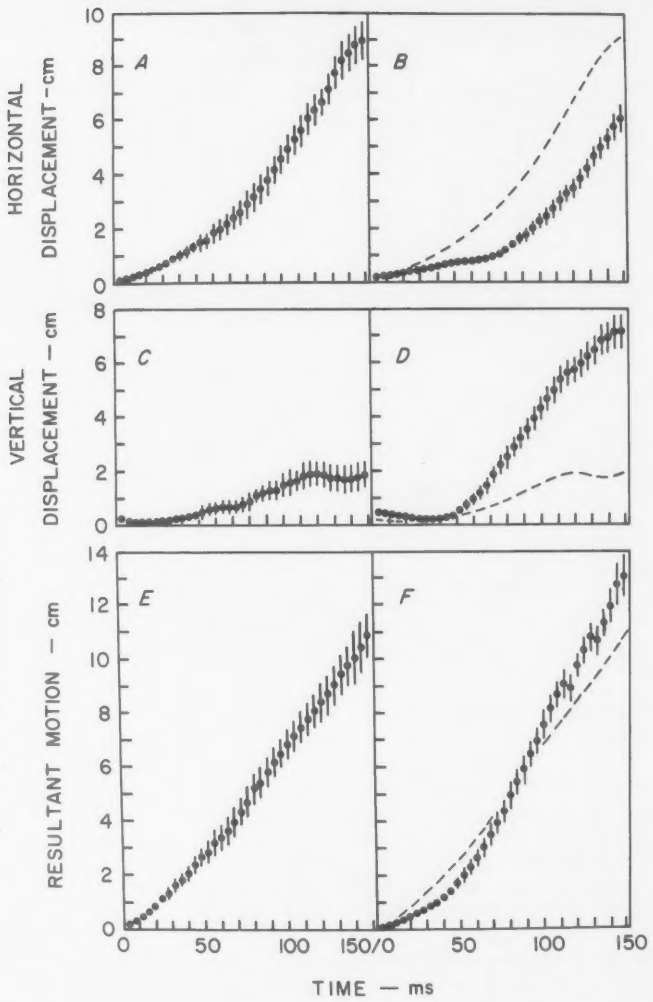

FIGURE 2.—Relationships between the distance traveled by the center of mass (the point about which propulsive forces act) and elapsed time during fast starts of *Citharichthys stigmaeus*. The motion of the center of mass was resolved into the distance traveled in the horizontal (A, B) and vertical (C, D) planes. These data were used to calculate the resultant distance traveled (E, F). Fast-start performance is shown for fish accelerating in the water column (A, C, E) and from the grid (B, D, F). The dotted lines in B, D, and F show the motions of the center of mass of fish accelerating in the water column from A, C, and E to facilitate comparison with fast starts from the grid. Vertical bars shown ±2 SE.

hydrodynamic ground effect influenced speckled sanddab fast starts. All data for fish accelerating from the grid were therefore combined for subsequent analysis and for comparison with fish accelerating in the water column.

The performance of fish accelerating from the grid differed from that of fish accelerating in the water column. The differences were seen in horizontal and vertical motions and in the net (resultant) motion. In the horizontal plane, fish accelerating from the grid traveled 0.8±0.2 cm in 63 ms at the end of stage 1, compared with 1.9±0.4 cm in the same time for fish accelerating in the water column. By the end of stage 2 fish starting from the grid had moved forward 3.9±0.9 cm in 124 ms. This was an improvement over stage 1, but still less than that of fish in the water column which moved forward 6.8±0.9 cm in the same time. The small initial displacement of fish in contact with the grid was probably due to frictional interactions between the fish and the grid (Arnold and Weihs 1978). The normal force at the point of con-

tact would also have been augmented by recoil forces generated by the tail and head tending to displace the fish downwards.

The motion of the center of mass in the vertical plane also differed between speckled sanddabs accelerating from the grid and in the water column (Figure 2C, D). For fish accelerating from the grid there was little vertical movement during fast-start stage 1 because of the presence of that grid. During stage 2, however, the center of mass was accelerated vertically upwards moving 6.0±2.4 cm in 124 ms. Fish accelerating in the water column showed little vertical motion, except that due to recoil (Figure 2C).

The resultant motion of the center of mass of the fish showed differences between acceleration in the water column and from the grid, but these differences were less marked than motions in the horizontal and vertical planes (Figure 2E, F). The increase in distance covered with time was initially greater for fish accelerating in the water column. They traveled a total of 3.7±0.6 cm in 63 ms compared with 2.9±0.4 cm for fish accelerating from the grid. However, once fish pushed against the grid in stage 2, performance improved. By the end of stage 2, they had traveled a cumulative distance of 10.2±1.2 cm in 124 ms, greater than that of 8.7±1.3 cm achieved by fish accelerating in the water column.

Velocities calculated for the center of mass reached maximum values close to the end of stage 2. Maximum values were significantly greater for fish accelerating from the grid compared with fish accelerating in the water column (Table 2). Mean acceleration rates would, of course, follow similar trends to velocities. Maximum acceleration rates only showed significantly improved performance for resultant motion of fish accelerating from the grid (Table 2).

TABLE 2.—Results of maximum acceleration rates and maximum velocities for *Citharichthys stigmaeus* accelerating from the grid and in the water column. Data (mean ±2 SE; $n = 10$) are shown for motion of the center of mass.

Item	Fast starts from the grid	Fast starts in the water column
Maximum acceleration rates, m/s²:		
Horizontal	37±7	48±10
Vertical	54±10	44±9
Resultant	66±12	46±12
Maximum velocities, m/s:		
Horizontal	66±11	92±10
Vertical	92±12	17±4
Resultant	104±17	76±14

DISCUSSION

These experiments show that the bottom (grid) does influence fast starts in speckled sanddabs. Fast starts from the bottom were associated with large amplitude motions that would normally cause substantial recoil of the center of mass because the bottom prevents that recoil. Motions of fish accelerating from bottom contact were predominantly vertical compared with horizontal motions of fish accelerating in the water column. The relative magnitude of vertical and horizontal displacements of sanddab accelerating from the grid are comparable with those observed in crayfish under similar circumstances (Webb 1979). For both speckled sanddab and crayfish the marked vertical motion is caused by prolonged contact between the body and the ground. Unfortunately, these large vertical displacements in speckled sanddabs preclude any significant hydrodynamic interaction with the ground after contact is lost.

Withers and Timko (1977) give a succinct explanation of this hydrodynamic ground effect, where the ground influences the flow, increasing lift (thrust) and decreasing drag. Hydrodynamic ground effect rapidly declines as the ratio, y/s, increases, where y is the gap between the surface generating thrust and the ground, and s is the span (width) of that surface. Blake (1979) found that 80-90% of the ground effect vanished by the time y/s reached unity in hovering mandarin fish. The mean maximum span of speckled sanddab, located at the center of mass, was 6.7±0.2 cm. For this span, $y/s = 1$ after about 130 ms, 18 ms after the end of physical contact with the bottom (Figure 2D). The caudal fin had a maximum span of 2.4±0.3 cm, and a value of $y/s = 1$ is reached within about 16 ms after the tail loses contact with the bottom (Figure 1A). Thus, the vertical acceleration rapidly lifts the speckled sanddab out of the hydrodynamic influence of the ground so that there is insufficient time for any interaction to affect performance. However, the absence of this effect during a fast start does not preclude hydrodynamic ground interactions from improving steady swimming close to the sea floor.

Thus, the observations on fast starts of speckled sanddab from the bottom show that a single kinematic pattern is used, which sustains bottom contact for most of a fast start, but which prevents development of any significant hydrodynamic ground effect. However, a direct push against a

solid substrate will always convert more muscle energy into body motion than working against a fluid. It therefore appears that speckled sanddab utilizes fast-start behavior that makes the greatest use of the available ground interaction options.

However, the interaction with the ground cannot be assumed to be adaptive before considering the question of advantages and disadvantages. For example, the small initial displacement of the center of mass of fish accelerating from the ground might be disadvantageous in some circumstances, such as escaping from predators. However, significant protection is achieved by camouflage and cryptic behavior in pleuronectiform fishes, rendering this contingency unlikely.

The influence of the bottom is clearly advantageous in the capture of elusive prey, a second behavior in which fast starts play a key role (Eaton and Bombardieri 1978; Webb and Skadsen 1980). Elusive prey, e.g., fish and crustacea, are common dietary items for pleuronectiform fishes in the families Psettodidae, Bothidae, and Pleuronectidae (Liem and Scott 1966; Norman 1966). The bottom eliminates recoil so that the fish can rapidly accelerate the head vertically (Figure 1). Continued rapid vertical acceleration is facilitated by prolonged bottom contact through the major acceleration period of a fast start. Bottom contact also results in the acquisition of a superior final speed that would be advantageous in a continued attack. The time taken to accelerate from the bottom and reach maximum speed could also be reduced by resting in sand in a curved U-shaped posture. This may occur since flatfish often dig into sand with the eyes and tail at the surface, but the body buried, implying a curved posture (Hobson 1979). Thus, the morphology and behavior of the benthic sanddab appear to be adaptive in improving fast-start performance, as well as for camouflage. Such advantages undoubtedly apply equally to other members of the pleuronectiformes and therefore provide an additional functional explanation of the unique flatfish body form and habits.

ACKNOWLEDGMENTS

This work was completed during the tenure of an NRC/NOAA Research Associateship. Fish were provided by the Naval Ocean Systems Center, San Diego. I thank J. R. Hunter and R. Lasker for their excellent comments on the manuscript.

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DAILY PATTERNS IN THE ACTIVITIES OF SWORDFISH, *XIPHIAS GLADIUS*, OBSERVED BY ACOUSTIC TELEMETRY

FRANCIS G. CAREY[1] AND BRUCE H. ROBISON[2]

ABSTRACT

Horizontal and vertical movements of swordfish were studied using acoustic telemetry. Five swordfish in the Pacific and one in the Atlantic were tagged with transmitters which provided information on location, depth, and surrounding water temperature. Two of the Pacific fish showed a clear daily cycle of movement between an inshore bank during the day and deep water offshore at night. All of the swordfish responded to light, swimming deep during the day and coming near the surface at night. In the Pacific depth during daylight appeared to be limited to about 100 m by the oxygen-minimum layer, but in well-oxygenated waters of the Atlantic, a midday depth of greater than 600 m was recorded and the fish appeared to follow an isolume. Depth of the Atlantic fish in daylight was related to changes in light caused by variation in water transparency. The vertical movements were associated with temperature changes of as much as 19° C within 2 hours. The implications of rapid vertical movements on buoyancy and swim bladder volume are discussed.

Despite their high commercial value and their significance as one of the large predators of the open ocean, relatively little is known about the habits and behavior of the swordfish, *Xiphias gladius*. The information which is available comes chiefly from observations made at the sea surface by commercial fishermen and from a few scientific studies based on commercial captures. Swordfish are large, fast-swimming fish that offer little opportunity for direct observation; however, some aspects of their behavior can be readily examined by telemetry from attached sensors.

Xiphias gladius is found throughout tropical and temperate waters. Its appearance in higher latitudes usually occurs in warm-season aggregations along the edge of the continental shelf and on offshore banks (Rich 1947; Wise and Davis 1973). The seasonal appearance of swordfish in both the western North Atlantic and Hawaiian fisheries (Uchiyama and Shomura 1974; Caddy[3]) coupled with the known distribution of their larvae and of adults with ripe gonads indicate a spawning migration to waters warmer than 23°-24° C (Arata 1954; Taning 1955; Gorbunova 1969; Markle 1974; Nishikawa and Ueyanagi 1974), while nonspawning fish appear to move between coastal and oceanic waters. Tagging studies show that some swordfish undertake long-distance movements. For example, a 12 kg swordfish tagged near the Mississippi Delta in March 1974 was recovered from Georges Bank at a weight of 86 kg in August 1977 (Casey[4]). The recovery of tagged swordfish near the point of release, even after several years at large (Beckett 1974), implies homing behavior if we assume that these fishes are regular migrators.

Longline fishery captures of swordfish occur primarily at night on hooks set at depths of 5-50 m. Deeper vertical excursions have been documented by DSV *Alvin* when the submersible was attacked by a swordfish at 610 m (Zarudski and Haedrich 1974) and by observation from *Deepstar* at 654 m (Church 1968). The harpoon fishery relies on the occurrence of swordfish near the surface during the day where they are commonly found resting in the warmer surface waters, often with their dorsal and upper caudal fins exposed. In this situation they can be approached and harpooned. This "basking" behavior may warm the fish and aid in the digestion of prey caught while foraging at greater depths. Spotter pilots for the harpoon fishery report that basking swordfish often defecate before sounding or breaching.

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[2]Marine Science Institute, University of California, Santa Barbara, CA 93106.
[3]Caddy, J. F. 1976. A review of some factors relevant to management of swordfish fisheries in the northwest Atlantic. Environ. Can., Fish. Mar. Serv., Tech. Rep. 633, 42 p.

[4]John G. Casey, Apex Predator Program, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882, pers. commun. 1978.

Manuscript accepted December 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

Examination of swordfish stomach contents (Scott and Tibbo 1968; Ovchinnikov 1970) showed that they feed on cephalopods and a wide variety of nektonic fishes (e.g., anchovies, hake, mackerel) and micronektonic fishes (e.g., myctophids, paralepidids) and that a significant portion of their diet consisted of vertically migratory mesopelagic species. We have also found unusual items in their stomachs including birds and shrimp. Swordfish have been observed swimming through schools of fish, stunning them with their swords before eating them (Goode 1883). Fish removed from swordfish stomachs often show damage to the muscle and vertebral column from having been hit by the sword (Scott and Tibbo 1968). Swordfish have large eyes and are efficient visual predators even in dim light. Small phosphorescent lights are occasionally used to attract them to longline hooks, which indicates that they may also respond to bioluminescence.

Swordfish are aggressive and there are many accounts of their attacking and ramming their bills into ships, whales, and other objects (Goode 1883; Gudger 1938; Smith 1956; Jonsgard 1962). We have seen penetrating wounds in swordfish and Edlin[5] found a 15 cm fragment of a swordfish bill that entered near the heart of a 70 kg swordfish and was driven back into the body cavity, which may indicate that they strike each other. While they are generally solitary, longline fishermen say that in the Straits of Florida, a spawning area, swordfish may be encountered in twos with some regularity.

In the present study we investigate the horizontal and vertical movements of swordfish during their daily activities and attempt to determine the range of temperatures they encounter. We used acoustic telemetry to monitor data from depth and temperature sensors attached to the fish for periods of up to 5 d. The results presented here provide the first description of their activities based on continuous direct observations of individuals.

METHODS

We attempted to attach transmitters to seven swordfish and were successful with five in the Pacific, near Cabo San Lucas at the tip of Baja California, and one in the Atlantic, east of Cape Hatteras, N.C.

For the experiments off Baja California, the swordfish were located on the surface by aircraft and the transmitters harpooned into the free-swimming fish from the tracking vessel *Sea World*. In the Atlantic, the swordfish were taken on commercial longline fishing gear set by the tracking vessel FV *Diane Marie*. Weights of the fish were estimated by the fishermen.

Transmitters

Two types of sensors were used in the transmitters. Depth transmitters had a 500 or 1,000 lb/in^{2}g Biotek[6] strain gage pressure transducer. Temperature transmitters had a 300 kΩ Fenwall GA53M2 thermistor linearized with a series resistor. An up-down integrating circuit converted resistance changes in the sensor to a varying pulse rate. The pulses keyed an oscillator and output stage which drove a 1.27 cm long, 2.79 cm (outer diameter) cylindrical ceramic transducer (Marine Research TCD 5) with 30 ms pulses of ultrasound at an electrical power level of one to several watts. The transducers, which were mechanically resonant at 33 kHz, were operated at 32 kHz for temperature and 34 kHz for depth so that signals could be separated in experiments where both were used simultaneously.

Power was supplied by a battery of five 1.2-Ah lithium cells (Mallory L0325) which give a useful life of about 1 wk. Range was as great as 3-5 km at times, but much shorter when propagation conditions were poor.

The transmitters were 14 cm long, 4.5 cm wide by 3 cm thick and weighed 250 g in air and 90 g in water. They were cast in a strong epoxy plastic (Hysol 2039 resin, 3561 hardener) and tested to withstand hydrostatic pressures equivalent to a depth of 1,000 m. A miniature (6.5 cm long) swordfish dart was tied to the end of the transmitter with a 13 cm loop of twisted 200-lb (91 kg) test monofilament nylon (Figure 1). An adapter which fitted on a standard swordfish harpoon had a crosspiece which limited penetration of the dart to about 10 cm. In some experiments depth and temperature transmitters were tied in tandem and attached to the fish with a single dart. The swordfish showed no obvious reaction to the tags once they were attached.

The instruments were stable and accurate.

[5]Robert Edlin, P.O. Box 341303, Coral Gables, FL 33134, pers. commun. 1980.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

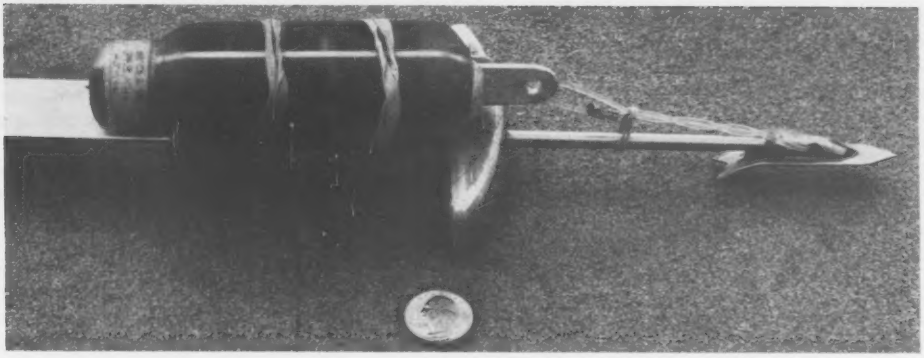

FIGURE 1.—Depth transmitter for swordfish. Rubber bands hold the transmitter to an adapter which fits on a standard swordfish harpoon. The crossbar on the adapter serves to limit penetration of the harpoon dart. A conductive path between two elements of a seawater switch turns the transmitter on when it enters the water. The coin is 24 mm in diameter.

Changing battery voltage did not affect the pulse rate of either type of transmitter, and the pulse rate of depth transmitters was not affected by temperature changes in the range 5°-30° C. In use we found that several days into an experiment the depth transmitters would still indicate <1 m when the fish was seen on the surface. A temperature transmitter recovered after 13 d on a fish was recalibrated and found to be within 0.1° C of the original calibration.

Receiving

We listened to the transmitters with a directional hydrophone constructed of seven ceramic transducer rings wired in parallel in a cylindrical array 10.5 cm long. The rings were backed with a layer of closed-cell polyethylene foam and cast in epoxy. A preamplifier in the hydrophone amplified the signal 100× and reduced problems from electrical noise picked up on the cables. The upper and rear surfaces of the horizontally mounted hydrophone cylinder were acoustically shielded with four alternating layers of 3 mm thick foam rubber and steel, leaving an approximately 140° sector uncovered and facing forward and down. The hydrophone was mounted at the bow of the vessel on a streamlined fin arranged so that it could pivot and follow the flow of water as the boat yawed. A shaft through the fin allowed the hydrophone to be rotated by a rope and pulley system from the bridge of the vessel.

The receivers (Lawson Instrument Company and CAI CR-40) were mounted on the bridge so that one person could follow the fish by rotating the hydrophone to find the strongest signal, then steering the boat in that direction. Data were recorded by timing a fixed number of pulses to the nearest 0.1 s with a stopwatch and converting the pulse rate to temperature or depth using a linear regression for the calibration curve. A 0.1 s counting error in a 30 s count produced a depth error of approximately 2 m. Data were taken routinely every 5 or 10 min and more frequently when the fish was changing depth. An automatic data recording system, based on a phase lock receiver, was used on 11 November 1977 and gave a continuous, detailed record of a swordfish rising to the surface in a series of steps.

Navigation

In the Baja California area we used radar to determine range and bearing to various peaks and headlands. The relative accuracy of this technique was good as checked by comparison of echo sounder depth with depth given on the chart at the plotted position. In the experiment near Cape Hatteras we used loran C with an accuracy better than 1 km. The position of the vessel was recorded when it was brought close to the fish and the plot of these positions used to approximate the fish's course.

Temperature

Temperature of the water was measured with expendable bathythermograph probes (XBT) (Sip-

pican T-6 and T-10) which were dropped routinely every several hours and more frequently when passing through boundaries between water masses. The XBT records were used to construct plots of isotherm depth. By superimposing the plot of swordfish depth on the isotherms, we could tell water temperature at the location of the fish in those experiments where a temperature transmitter was not used.

RESULTS

Swordfish No. 2, 19-24 April 1977, Baja California, Mexico

This 70 kg swordfish sounded when struck with the transmitter, but quickly came up and spent 20 min on the surface. It appeared to be in good condition and unaffected by the depth transmitter. During a 5-d period it showed a clear cyclical pattern of movement between an inshore bank during the day and offshore waters at night (Figure 2). Each day it occupied the same area along the 50-fathom (91 m) depth contour on the bank. Several hours before sunset it would move offshore, going out as far as 26 km from land, and remain in deep water all night. At first light of dawn, 1.0-1.5 h before sunrise, it would swim inshore again and return to the 50-fathom contour on the bank.

The fish remained close to the bottom while on the bank, coming to the surface during daylight only three times in 5 d. On 20 April it was usually 5-10 m up from the bottom and on the following days, usually 5-20 m above it. Each evening, an hour after sunset, swordfish no. 2 rose to the surface and spent the night in the upper 10 m. At first light, an hour before dawn, it descended and moved toward shore at depth with frequent vertical excursions.

Swordfish No. 3, 26-27 April 1977, Baja California, Mexico

This 70 kg fish was found close to where no. 2 had been tagged and was harpooned with both depth and temperature transmitters. It followed a similar pattern to no. 2, moving offshore before sunset and turning inshore at first light (Figure 3). Several hours before sunset both of these fish would leave their position on the 50-fathom contour of the bank and swim offshore into deeper water. They swam twice as fast, perhaps 3 km/h, when moving offshore as they had while on the bank. When on the surface several hours after dark, swimming speed usually slowed to 1 or 2 km/h. The movements during the dark hours showed a distinct offshore progression ending at an average distance of about 19 km offshore where the fish moved about slowly until first light. The journey back to the bank was again at a higher speed, about 3 km/h.

From 1100 to 1800 h on the second day, no. 3 remained in one spot and appeared to be resting on the bottom during part of this time (determined by positioning the boat over the fish and noting that the echo sounder depth was the same as that telemetered from the fish). At sunset it rose from the bottom and headed offshore. We lost it soon afterward when our equipment was damaged in rough water.

Swordfish No. 4, 30 April 1977, Baja California, Mexico

This 80 kg fish was harpooned in midmorning in 500 m of water some 24 km off the coast. It moved slowly in a westerly direction (Figure 4) staying uncharacteristically near the surface, frequently with its fins showing, and did not descend below 10 m. It was followed for only 2 h, then abandoned because of technical problems.

Swordfish No. 5, 30 April 1977, Baja California, Mexico

This fish weighed about 100 kg and was harpooned close to where we left no. 4. It also moved slowly westward, covering <3 km in the first 5 h (Figure 4). An hour before sunset it turned south and swam offshore over San Jose Canyon at a speed of 3.5 km/h. During the day it surfaced five times, spending alternate periods on the surface and at 100 m. Sunset marked a period of vertical activity and a gradual ascent to the upper 25-50 m. We lost the fish in rough weather that night as it was swimming offshore on a southerly course.

Swordfish No. 6, 3-6 May 1977, Baja California, Mexico

Swordfish no. 6 weighed about 140 kg and was harpooned with depth and temperature transmitters in an area about 24 km offshore, near where no. 4 and 5 had been tagged (Figure 4). It swam slowly westward as those fish had done,

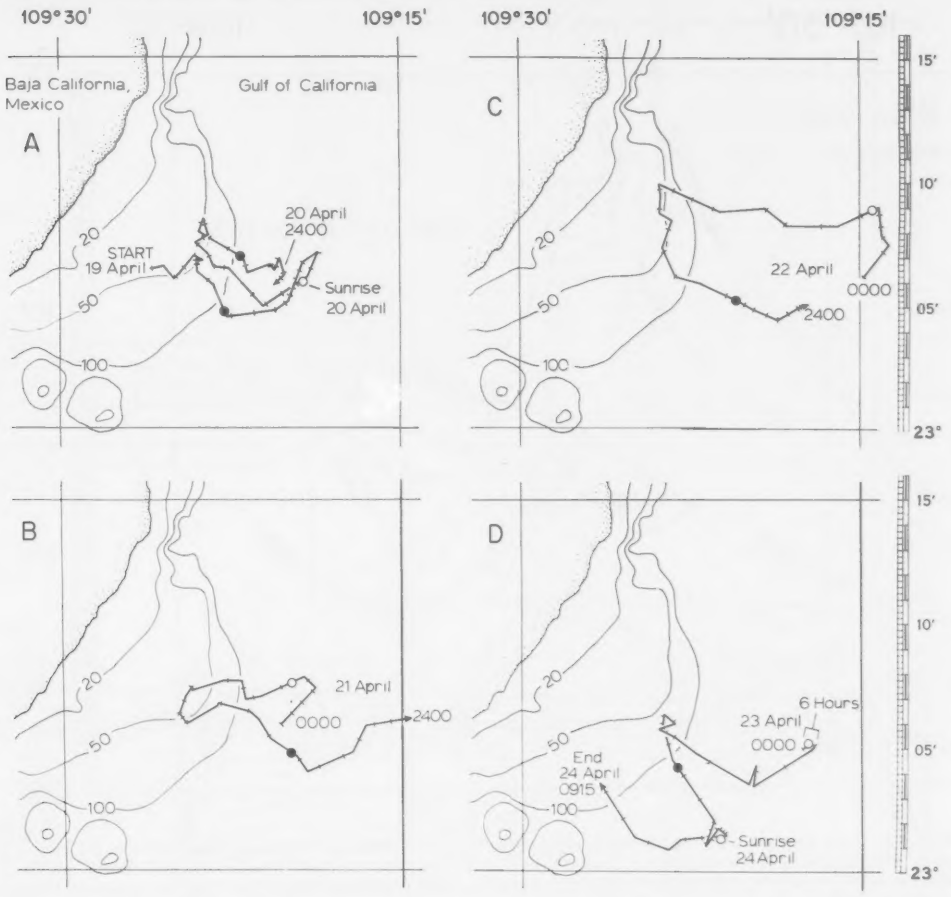

FIGURE 2.—Track of swordfish no. 2, Baja California, separated into four panels for clarity. Each day this fish moved inshore to the 50-fathom (91 m) curve on a bank then moved out over deep water at night. The turn inshore began about 1 h before dawn; the offshore movement began several hours before sunset. Compare with the depth record in Figure 9. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in fathoms.

moving 9 km in 5 h, then turned to the south at sunset and moved down the axis of San Jose Canyon. It continued in a southwest direction when it reached deep (2,000 m) water, and by dawn on 6 May when we abandoned it, it had gone 88 km in 44 h.

No. 6 showed the now-familiar pattern of vertical movements, staying near the surface at night and going deep during the day (Figure 5). Like no. 5 it made excursions to the surface during daylight hours, coming up five times to spend periods of 0.5-1.5 h on the surface, then returning to depths which averaged 75-100 m, but included much deeper excursions.

While on the surface during the day, no. 5 and 6 swam about actively. No. 6 moved at an estimated 1.6-3.2 km/h (1-2 kn) in a haphazard pattern with much turning, so that progression along its course was considerably slower than its swimming speed. It appeared to be responsive and moved after a live Pacific mackerel, *Scomber japonicus*, which was thrown to it. On one occasion we attempted to

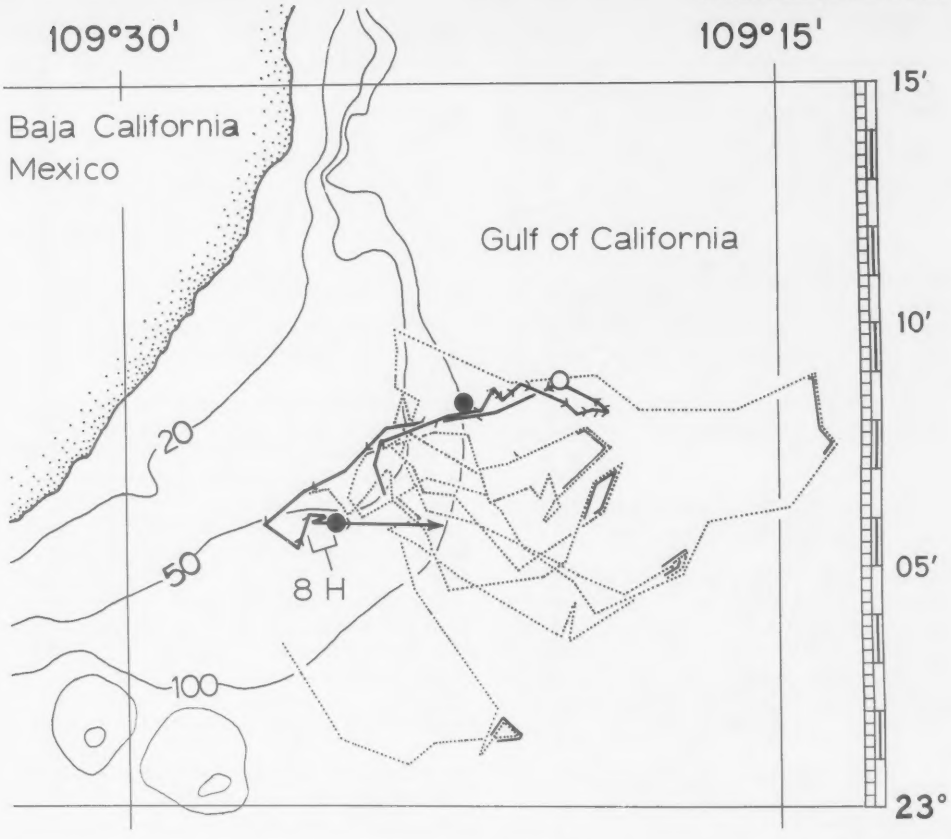

FIGURE 3.—Track of swordfish no. 3 (solid line) superimposed on track of swordfish no. 2 (dotted line), Baja California. No. 3 was on the bottom during much of the indicated 8-h period. The narrow solid lines near the track (dotted line) of no. 2 indicate positions where it was moving slowly on the surface at night. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in fathoms.

drive it down with the boat, but it sank just a few meters and avoided us. When hard pressed, it easily escaped in a series of long horizontal leaps, but did not go below a few meters depth until it had been on the surface for about 1 h.

Swordfish No. 7, 9-11 November 1977, Atlantic Ocean

This 70 kg swordfish was taken by longline about 100 km northeast of Cape Hatteras (lat. 36°00′ N, long. 74°40′ W) in a depth of 1,000 m (Figure 6). The fishing gear was left in the water for only 1 h to reduce the time that the fish would be struggling on the line. The fish was hooked in the tip of the lower jaw, a place where little damage would be expected; its bluish color and active movement gave the impression that it was in good condition. It was tagged with a depth transmitter and cut free within about 15 s after it had been brought alongside the boat.

The longline had been set in a patch of warm blue water (Figures 6, 7). When released the fish swam in a general southeast direction, a course which took it under a tongue of cold, grey-green shelf water. After several course changes, it came out from under this cold water on the second day and entered the Gulf Stream which swept it to

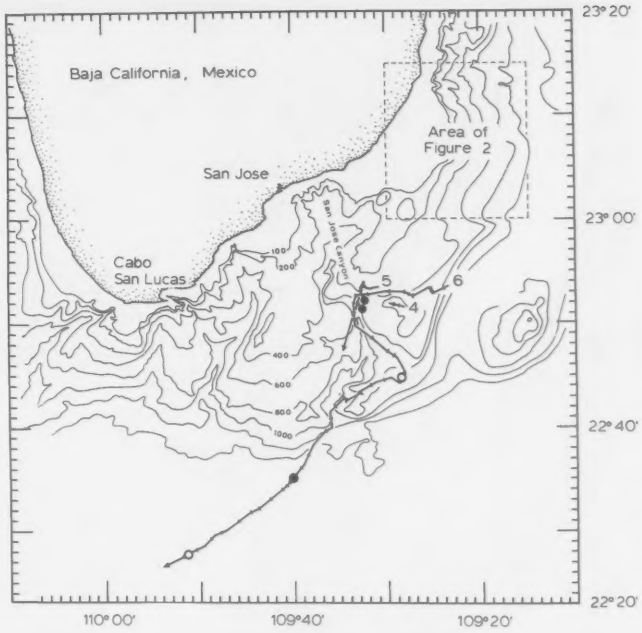

FIGURE 4.—Track of swordfish no. 4, 5, and 6, Baja California. These fish all moved west during the first afternoon; no. 5 and 6 then moved down the axis of San Jose Canyon after sunset. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contours in meters.

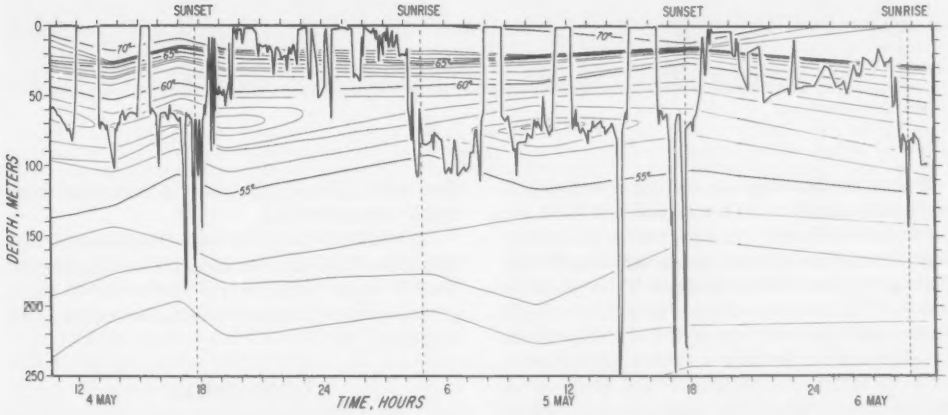

FIGURE 5.—Depth record for swordfish no. 6 off the tip of Baja California superimposed on an isotherm pattern drawn from bathythermograph lowerings. There was a full moon during this experiment and the usual nighttime depths were deeper than those on the moonless nights during experiments with swordfish no. 2 and 3. The fish generally swam below the thermocline during the day and was well into the oxygen-minimum layer, where oxygen concentration was estimated to be about 10% that on the surface. Isotherm interval 1° F.

the northeast. At the end of the third day the flattening of the deep isotherms (Figure 8) indicated that it had crossed the center of the Gulf Stream and entered the Sargasso Sea. When we abandoned the fish it had gone a distance of 240 km in 67 h.

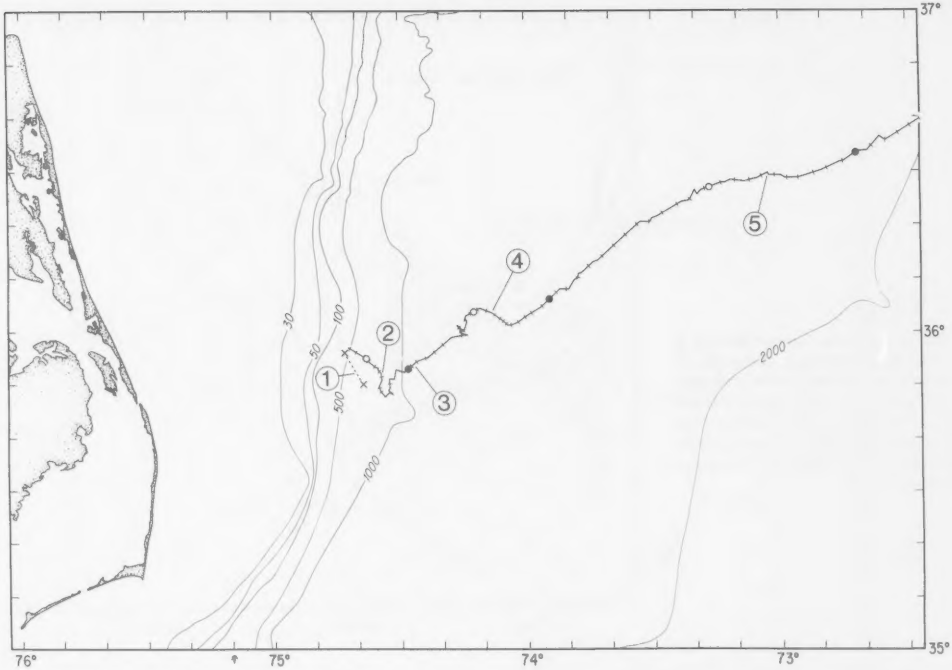

FIGURE 6.—Track of swordfish no. 7 in the Atlantic near Cape Hatteras, N.C. 1) Dotted line indicates position of longline gear where this fish was caught. 2) The swordfish moved beneath a layer of cold surface water at 1000 h on 9 November. 3) It emerged from beneath the cold surface layer at 2000 h on 9 November. 4) By 0500 h 10 November, it was in the Gulf Stream. 5) At 1500 h 11 November, it had crossed the Gulf Stream and entered the Sargasso Sea. Dots represent sunset; circles represent sunrise. Ticks at 1-h intervals, bottom contour lines in fathoms.

During the first day, the vertical movements of no. 7 were complex. On the second and third day however, it followed a clear pattern of moving near the surface at night and going deep during the day. An hour before dawn on 10 November it was in 27° C water at a depth of 20 m (Figure 8). It began to descend and was in 8° C water at 400 m 2 h after sunrise. An hour before sunset it started back toward the surface and was at 20 m at twilight. No. 7 spent the night at about 20 m with four brief excursions to 100 m. Some of these were caused by our tracking vessel, for swordfish would often dive when we drove the boat over them and would do this even at night when the ship was darkened. The depth pattern on 11 November was similar to the previous day. Leaving the surface 1 h before dawn, it descended rapidly and was at 450 m shortly after sunrise. It continued to descend, reaching 617 m at noon, then starting back up, slowly at first, then more rapidly around sunset.

A continuous recording of the final ascent, made with the phase lock receiver, shows that it was done in steps with a rapid rise of 20-80 m, a pause for several minutes, then another rapid rise (Figure 8).

DISCUSSION

Horizontal Movements

Swordfish no. 2 and 3 showed clear cycles of movement between deep water and an inshore bank. During the day they occupied a rather narrow region, perhaps 8 by 1.5 km, along the 50-fathom (91 m) contour on the bank where the bottom fell off to the south and east (Figure 3). They stayed close to the bottom, moving slowly,

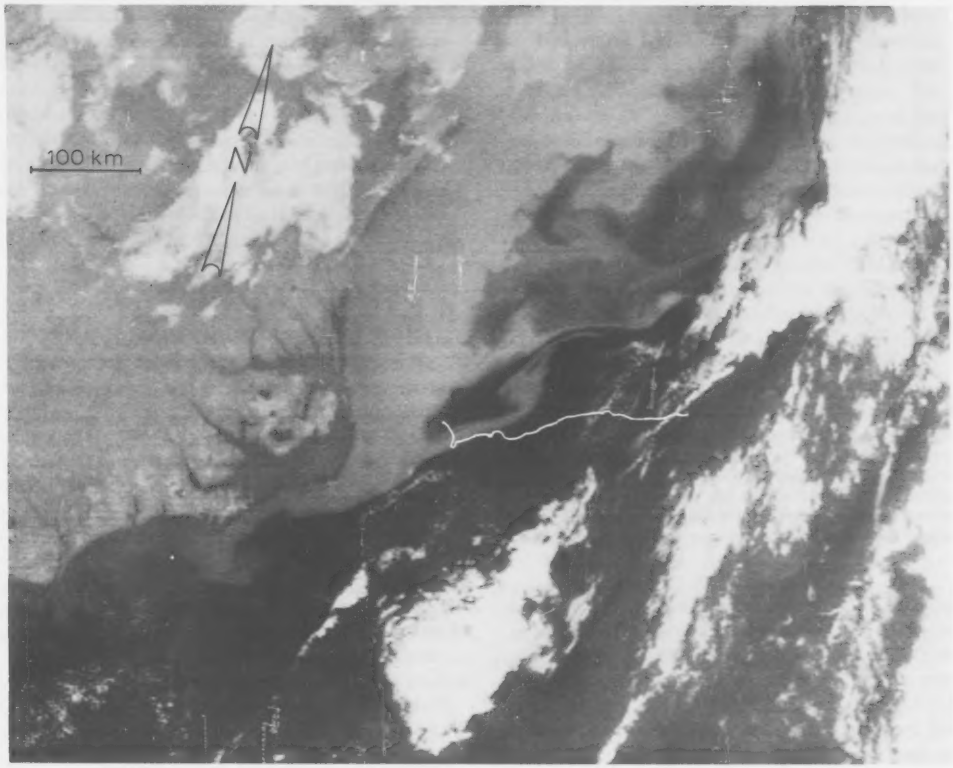

FIGURE 7.—Satellite infrared image of the Atlantic east of Cape Hatteras, N.C. (left center), with track of swordfish no. 7 superimposed. Light areas indicate cold water and dark areas warm water. The Gulf Stream moving past Cape Hatteras pulls off a streamer of cold shelf water. Swordfish no. 7 was tagged on the north side of this streamer, swam under it (see Figure 8), and crossed the Gulf Stream into the Sargasso Sea.

and may at times have been resting on it. Swordfish commonly feed on bottomfish (Scott and Tibbo 1968), and this location may have allowed them to prey on demersal fish moving on and off the bank.

In the evening no. 2 and 3 swam rapidly offshore and spent the night moving slowly in positions about 20 km from the coast (Figures 2, 3). A different area was visited each night, but they returned to the same spot on the bank every day. Squid, which were abundant on the surface at night, came to our lights in large numbers when we stopped. It is likely that the swordfish moved offshore to feed on the squid and other vertically migrating fauna which concentrate near the surface at night. The onshore-offshore movements which we observed may have been a feeding routine which allowed the swordfish to prey on demersal fish available in a prescribed spot on the bank during the day and to feed on squid and other prey wherever they were found over deep water at night.

In an area near Hawaii, Yuen (1970) used an acoustic transmitter to follow a skipjack tuna, *Katsuwonus pelamis*, for an 8-d period. He found that the fish remained with its school which spent the day on a bank and moved out over deep water at night. The nighttime positions were 20-100 km away from the bank, and like swordfish no. 2 and 3, a different area was visited each night. The behavior of the school during the day suggested to Yuen that the fish were foraging. A diel inshore-offshore movement cycle in the blue shark, *Prionace glauca*, near Catalina Island was reported by Sciarrotta and Nelson (1977). This cycle was

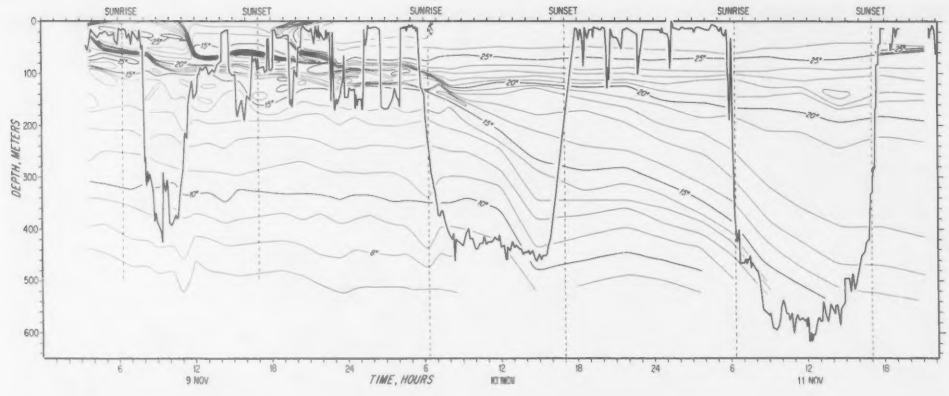

FIGURE 8.—Depth record for swordfish no. 7 off Cape Hatteras in the Atlantic superimposed on a 1° C isotherm plot drawn from expendable bathythermograph casts. On 9 November the fish passed under a cold streamer of shelf water (see Figure 7) and rose toward the surface in the middle of the day, probably in response to the decreased light. On 10 November the deepening isotherms indicate that the fish was following an isolume, descending 1 h before dawn, reaching its greatest depth at midday and coming to the surface 1 h after sunset. Continuous recording of depth on 11 November shows that the rise toward the surface at sunset was made as a series of steps with several minute pauses at each level. The flattening isotherms toward the end of the record indicate that the fish had entered the Sargasso Sea.

opposite in phase to that of the skipjack tuna and swordfish, with the sharks coming inshore at night. The authors suggested that the movements were associated with the nighttime availability of squid near the beach. It is likely that all of these diel cycles of movement are linked to changes in the location and availability of food.

Swordfish no. 4, 5, and 6, which were offshore in water 400-800 m deep, moved slowly west after they had been harpooned (Figure 4). We abandoned no. 4, but no. 5 and 6 continued until they were over San Jose Canyon, the most prominent submarine canyon in the area. Near nightfall, both of these swordfish changed course and moved south along the length of the canyon. The correspondence with the axis of the canyon is not exact, but the course change and the movement of both fish along the canyon suggests they were responding to the bottom topography. Commercial longline fishermen feel that the submarine canyons and hummocky areas along the edge of the continental shelf are good places to find swordfish.

Currents flowing over rough bottom produce eddies and flow separation features which may extend to the surface. The patterns of such turbulent flow affect the distribution of biological sound scattering particles and produce concentrations of organisms which can be seen in 200 kHz echograms made over Hudson Canyon in the Atlantic (Orr[7]). The concentration of organisms as a result of turbulence generated by the rough bottom may be the feature that attracts swordfish to the waters over submarine canyons.

Fishermen had suggested that swordfish in the area where no. 2 and 3 were followed were part of a resident population, while those in the area of no. 4, 5, and 6 were transient. Our results are consistent with this notion.

In the Atlantic, swordfish no. 7 swam in a southeasterly direction at a speed of 1.5-2.0 km/h during the first day. On the second day it entered the Gulf Stream as indicated by the deepening of the isotherms in Figure 8. While in the Gulf Stream it moved on a course a little north of east at a speed of 5.5 km/h, with most of this velocity contributed by the current which was flowing northeast. The course of the fish was to the south of the direction of the current, indicating that there was a southerly component to its swimming. It probably continued to swim on its original course and speed after entering the Gulf Stream. By the time we abandoned it on the third day, it had crossed the Gulf Stream, which is about 75 km wide at this point, and entered the Sargasso Sea. This can be seen from the flattening of the deep

[7]Marshall Orr, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1980, manuscr. in prep.

isotherms at the end of the track in Figure 8 and from the position of the Gulf Stream indicated on the 9 November 1977 Experimental Ocean Frontal Analysis Chart.[8] Swordfish concentrate along the edge of the continental shelf, but are widely distributed over the ocean. The course that no. 7 followed may have been a normal one for swordfish in the Hatteras area, or no. 7 may have been influenced to swim offshore by the trauma of being caught on longline fishing gear.

Vertical Movements and Light

The tagged swordfish showed a clear diel pattern of vertical movements, going deep during the daylight hours and coming to the surface at night (Figures 5, 8, 9). This is best illustrated by swordfish no. 7 on 11 November (Figure 8). The fish spent the night at about 20 m. About 1 h before dawn, when light was just noticeable in the east, it swam down rapidly, reaching a depth of 400 m by sunrise, and worked gradually deeper until it reached 617 m at midday. After noon the swordfish gradually rose again, increasing its rate of ascent sharply around sunset and reaching the surface about 1 h later.

There is an obvious relationship between the vertical movements of swordfish and light. The most rapid changes in depth were during a 2-h period at dawn and dusk when surface illumination changes by six or seven orders of magnitude (Brown 1952), and the greatest depth was reached at noon when light at the surface was at a maximum. The U-shaped pattern of the depth curve would be expected for an animal following an isolume (Blaxter and Parrish 1965; Boden and Kampa 1967).

The swordfish also appeared to respond to moonlight. There was no moon during experiment 2 (new moon, 21 April) and only a thin crescent for swordfish no. 3. On these nights, which were starlit and calm, the swordfish were usually at depths <10 m and often right on the surface (Figure 9). In the other experiments there was a full moon shining through clouds and it was windier. Nighttime depths for no. 5 and 6 were 10-50 m (Figure 5) and for no. 7 about 25 m (Figure 8). The fish were probably swimming at a greater depth in response to moonlight, although the wind might also have had an influence.

Guitart Manday (1964) analyzed the depth at which swordfish were taken in a Cuban fishery at various phases of the moon. He concluded that moonlight did not affect vertical migration, but noted that the fishermen felt that the phase of the moon was important and there is some suggestion in his data that fish were taken deeper during the full moon. Tesch (1978) used acoustic transmitters to follow the silver eel stage of *Anguilla anguilla* and reported that one which swam at a depth of 100 m while the moon was up rose to 50 m when the moon set. Our similar records for swordfish suggest that they also respond to moonlight.

If swordfish move vertically to maintain a constant level of illumination, the light level they follow should be somewhat greater than that on the clear, starry nights when they came to the surface and somewhat less than in moonlight when they swam at 10-50 m depth. We may use the values for irradiance of 3×10^{-1} μW/cm^2 under a clear night sky with full moon, 3×10^{-3} μW/cm^2 for a clear sky with no moon, and 3×10^{-4} μW/cm^2 for a dark night from Clarke and Kelly (1964). At noon, 11 November 1977, swordfish no. 7 was at lat. 35° N and at a depth of 600 m. Surface illumination, I_0, for this time, recorded in Woods Hole and corrected for latitude, was 5×10^4 μW/cm^2 (Payne[9]). Light, I, at depth, L, of the fish can be calculated assuming an attenuation coefficient, k, of 0.028 for the clear Gulf Stream-Sargasso Sea water in this area, (Clarke and Backus 1964). The relationship

$$I = I_0 e^{-kL}$$

gives 2.5×10^{-3} μW/cm^2, a value similar to that on a clear, moonless night when the fish might be expected to come to the surface. The fact that swordfish may also come to the surface during the day indicates that they are not locked to an isolume, but under some conditions they do appear to adjust their vertical position in a manner which would maintain a constant, dim illumination throughout the day.

Vision is obviously important to swordfish. The eyes of a 150 kg fish are as large as an orange and almost touch in the midplane of the skull. The amount of light we calculate for the isolume followed by swordfish is many orders of magnitude greater than the 3×10^{-10} μW/cm^2 suggested as a

[8]U.S. Navy Oceanographic Office NSTL Station, Bay St. Louis, MS 39522.

[9]R. E. Payne, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1977.

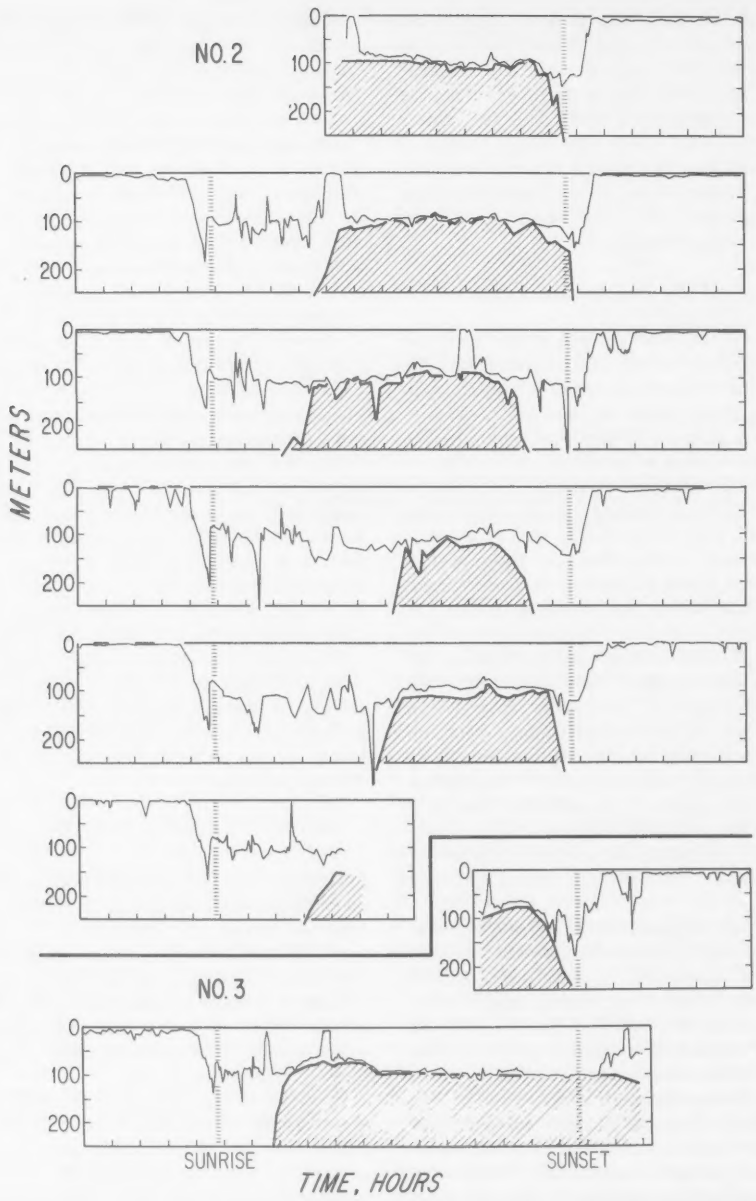

FIGURE 9.—Depth records for swordfish no. 2 and 3, Baja California, plotted from midnight to midnight. The crosshatched area indicates a bank. The fish swam near the surface at night and at a depth of about 100 m during the day. The morning dive about 1 h before sunrise carried the fish below its usual daytime depth.

threshold for vision in deep-sea fish (Denton and Warren 1957; Clarke and Denton 1962). The swordfish should be able to locate its prey visually in its dimly lit environment both day and night.

Our depth records for swordfish show many variations from the U-shaped pattern expected if they are following isolumes. Much of this variation can be explained as modification of a response to light by other environmental factors. On 10 November the depth record for no. 7 was skewed, with the greatest depth reached late in the afternoon (Figure 8). The deepening isotherms during this day indicate that the fish was moving from shelf and slope water into the warm, clear water of the Gulf Stream. Light attenuation is much greater inshore than in the Gulf Stream (Jerlov 1968) where the same level of illumination occurs at greater depths. The gradual increase in depth during the fading daylight on this afternoon coincided with the movement from slope to Gulf Stream water and can be interpreted as the fish maneuvering deeper to maintain a constant light intensity in the clearer water.

On 9 November, no. 7, which had reached 400 m by midmorning, returned to 100 m at noon. This unexpected midday rise from depth occurred when the fish left a region of clear blue slope water and passed under a streamer of dark grey-green shelf water (indicated as a marked thermal inversion in Figure 8 and as a light-colored region in the satellite infrared image, Figure 7). Swimming under this dark shelf water, the swordfish entered a shadowed area. By rising toward the surface it would have returned to a light level which prevailed at greater depth in the blue water. A change of attenuation coefficient from 0.035 in blue water to 0.140 in shelf water would result in the same light intensity at 400 m as at 100 m depths, respectively. These are reasonable attenuation values and it is possible that the swordfish was maintaining a constant light level during this vertical movement.

Oxygen

A vertical movement in response to sunrise and sunset occurred in all of the Baja California experiments. An interesting feature is apparent when these depth records are aligned vertically (Figure 9). The rapid descent which began about an hour before dawn each morning reversed at sunrise when the fish came back up to about 100 m. A well-developed oxygen-minimum layer exists in this area of the eastern tropical Pacific and the oxycline at the top of the low oxygen region is parallel to the thermocline, but at somewhat greater depth (Griffiths 1968, fig. 11 and 27). In its normal movement away from the surface with increasing light at dawn, the swordfish penetrated deeply into this low oxygen layer, then returned to spend most of the day at shallower depths with higher oxygen concentration. The presence of the oxygen-minimum layer caused the swordfish to spend the day at a shallower depth and higher light level than normal.

In Baja California swordfish frequently came up during the day to bask on the surface with the tips of their dorsal and caudal fins out of the water for periods of 15-80 min. This basking behavior, at a time of day when we would expect them to be at their greatest depth, may be related to the low oxygen concentration at depth. The depth record for no. 6 superimposed on an isotherm pattern in Figure 5 shows that the fish was well below the thermocline during much of the day. We did not measure oxygen, but using the data in Griffiths (1968) we can infer concentrations from water temperature and depth. When swordfish no. 5 and 6 were below the thermocline, they were in an environment with an oxygen concentration only 10 to 20% that of air-saturated water. This is a much lower concentration than the 60% saturation suggested as the lower limit for skipjack tuna in the vicinity of an oxygen-minimum layer (Ingham et al. 1977). The less active swordfish, with its large mass of white muscle, might be more resistant to anoxia and able to accumulate an oxygen debt. If so, the periodic excursions to well-aerated surface waters would allow it to recover from anoxia. There appears to be a rough correlation between time spent on the surface and the length of the preceding period below the thermocline, as would be expected if this were a recovery process: $T_S = 0.2\ T_L + 16$ ($r = 0.6$; $n = 10$) where T_S is time on surface in minutes and T_L is time at depth in minutes.

In the Baja California area, there was a marked difference between frequencies at which the inshore and offshore swordfish came to the surface during the day. The inshore fish surfaced six times in 7 d and spent 2.8% of the daylight hours on the surface. The offshore fish surfaced 10 times in 2.5 d, spending 25.7% of the daylight hours on the surface. This difference may be related to oxygen concentrations, for the inshore fish were near the mouth of the Gulf of California where the oxygen-

minimum layer is not well developed. They would probably encounter less anoxic conditions than the offshore fish which were well into the Pacific. Because of this, an attempt to compare abundance of swordfish in these two areas from the numbers seen on the surface could be grossly misleading.

On the continental shelf off the northeastern United States and Canada where swordfish can be seen "finning" on the surface during the warm months, the water is well oxygenated from surface to bottom. However, temperatures on the bottom can be quite cold, and the swordfish which are feeding deep may be coming to the surface to warm their muscles or as an aid in digestion. Basking behavior by swordfish may be part of a recovery from a variety of stresses experienced at depth.

Buoyancy

Swordfish swimming on the surface seem to have neutral or sufficient positive buoyancy to raise the dorsal and caudal fins out of the water. Swordfish taken on longline frequently float, swim bladders distended, when hauled to the surface, and would have been at neutral buoyancy at a pressure of a few atmospheres. The swordfish are clearly able to inflate their bladder to a volume which will give them neutral density at some near-surface depth. The capillary retia mirabilia of the gas gland are short, about 1 mm long, and similar to those of surface dwellers such as the flying fish (Marshall 1960, see footnote 10). Thus the structure of the gas gland does not seem suitable for rapid pumping of large volumes of oxygen under pressures up to 60 atm at 600 m. Our depth records (Figures 5, 8) show many examples of rapid vertical movements with the fish sometimes moving from 100 m to the surface in < 5 min. Such changes in depth could cause a 10-fold expansion in the volume of a free bubble. It seems unlikely that the swordfish could pump gas into and out of its swim bladder rapidly enough to maintain constant volume during these excursions. The necessity for doing this could be avoided if the bladder were allowed to compress with hydrostatic pressure as the depth increased. This would increase the density of the fish, but even with the bladder partially collapsed at depth, the high lipid content and porous fatty bone of the swordfish would lower its density and the flattened bill and fixed pectoral fins would give it hydrodynamic lift while swimming.

When at rest at depth, excess density would prevent the swordfish from hovering easily and it might find resting on the bottom to be a convenient position. While on the bottom the fixed pectoral fins would form an effective tripod with the tail (R. H. Backus[11]). Frequent records of swordfish caught in bottom trawls indicate that resting on the bottom may be common in this species (Bigelow and Schroeder 1953; Eschmeyer 1963). Martin Bowen,[12] a National Marine Fisheries Service (NMFS) observer on foreign squid trawling vessels working between Cape Hatteras and Cape Cod, Mass., reported 28 swordfish taken in bottom trawls during 72 d at sea in 1977. Observers in research submarines have seen swordfish lying on the bottom (Zarudski and Haedrich 1974), and in our records it appears that swordfish no. 3 was on the bottom for several hours.

Temperature

Water temperatures encountered by swordfish in the Baja California area are illustrated in Figure 5. A 10° C (18° F) gradient was present between the surface and the depth of the deepest dive, 300 m. The gradient between surface and the usual daytime depth was 5°-7° C. The fish made frequent excursions through the thermocline, passing such gradients in a few minutes. While these are significant temperature changes, they did not seem to affect the activities of the fish, which in this area appear to be more influenced by the presence of anoxic water.

Our record for swordfish no. 7 in the North Atlantic shows the impressive ability of this species to penetrate marked thermal boundaries (Figure 8). The greatest temperature change occurred on the morning of 10 November when this fish moved from 27° C water on the surface to 8° C water at 420 m, a 19° C excursion in 2.5 h. This is a large change for any heterothermal organism to undergo and remain active. It was not just a brief excursion, for it remained in the cold water all day. The thermal history of the fish before this dive was complex, but the preceding

[10] N. B. Marshall, Park Lane, Saffron Walden, Essex, Engl., pers. commun. 1975.

[11] R. H. Backus, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. 1972.

[12] M. Bowen, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543, pers. commun. 1978.

4.5 h included 1.5 h at 27° C, 1.5 h at 14° C, and 1.5 h at 27° C for an average water temperature of 22°-23° C before the descent. The swordfish is clearly able to function over a wide range of ambient temperatures.

The coldest water which no. 7 entered was 8° C. This may represent a lower preferred limit for swordfish, as it agrees with the 8° C temperatures reported for deeper sightings from research submarines (Zarudski and Haedrich 1974). The 8° C temperature may only be coincident with a light or depth limit or the location of prey; we look forward to experiments with swordfish in areas where water <8° C is readily available.

ACKNOWLEDGMENTS

This work was supported by a grant from the Culpeper Foundation; by a contract from NMFS, NOAA; and by grant PCM76-81612 from the National Science Foundation. The experiments could not have been done without the swordfish provided to us by Captain Bob Vile, pilot Pat Utely, and owner Milton Shedd of *Sea World*; and Captain Jimmy Ruhle and the crew of *Diane Marie*. We thank the fishery officials of Baja California Sur, Mexico, for permission to work in that area; Jack Casey, Northeast Fisheries Center Narragansett Laboratory, NMFS, NOAA, for his support and encouragement; and Captain Martin Bartlett, John Kanwisher, and many other fishermen and scientists of the Woods Hole community who donated time and materials and provided an atmosphere which made this project possible.

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GROWTH RATES OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, BASED ON TAG RETURNS

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ABSTRACT

Estimates of growth parameters for North Pacific albacore, *Thunnus alalunga*, were based on tag-recapture statistics, using the standard von Bertalanffy model and an extended model. Sequential estimation of L_∞ and K allowed us to test hypotheses concerning variation in growth rate between tagged albacore recaptured in different ocean regions.

Significantly lower growth rates were found in albacore recaptured off Japan and the United States north of latitude 40° north compared with those recaptured off the United States south of latitude 40° north. The differences in estimated growth rate were generally consistent with differences in length-frequency distributions of albacore taken off the United States north and south of latitude 38° north during the period when most recaptures were made. The findings add to a growing body of evidence that the North Pacific albacore population is not homogeneous; rather, at least two different subpopulations may exist.

Growth rates of North Pacific albacore, *Thunnus alalunga* (Bonnaterre), have been estimated by counting vertebral rings (Uno 1936; Aikawa and Kato 1938; Partlo 1955), examining scale circuli (Nose et al. 1957; Bell 1962; Yabuta and Yukinawa 1963), tracing progressions of length modes (Brock 1943; Suda 1954), and by measuring tagged fish at release and recapture (Otsu 1960; Clemens 1961). Of these techniques, only tagging provides direct estimates of growth rate, and the tagging results of Otsu and Clemens are reasonably consistent with the conclusions of Yabuta and Yukinawa's scale analysis and Suda's modal progression work. However, as Shomura (1966) noted in a review of tuna growth studies, comparisons are complicated by the biases and uncertainties peculiar to each method. For example, in the case of tagging we assume that the growth rate is unaffected by stresses resulting from capture, handling and tagging, and from the burden of carrying the tag itself. Conclusive results will require that the basic assumptions of any particular method be tested and verified.

In this paper, we present new estimates of growth parameters based on recent tag-recapture experiments conducted jointly by the National Marine Fisheries Service (NMFS) and the American Fishermen's Research Foundation (AFRF).[3] We use the standard von Bertalanffy growth model, but also briefly explore an extension. Sequential estimation of the parameters L_∞ and K allows us to test hypotheses concerning variation in growth rate between tagged fish recaptured in different ocean regions.

Transpacific recaptures of albacore tagged in the eastern North Pacific off North America and in the western North Pacific off Japan have established the interdependence of the United States and Japanese North Pacific albacore fisheries, and have also fostered the hypothesis of a single, common stock (Ganssle and Clemens 1953; Clemens 1961; Otsu and Uchida 1963). However, our results add to growing evidence (Laurs and Lynn 1977) that the North Pacific albacore population is not homogeneous, as usually assumed, but is composed of at least two subgroups with different migration patterns and growth histories.

METHODS

Tagging Procedures

Albacore were caught in the eastern North Pacific and tagged aboard U.S. commercial jig and

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Manuscript accepted December 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

[3]AFRF administers revenues derived from a landing assessment paid by the U.S. albacore industry on U.S.-caught albacore.

bait fishing vessels on charter to AFRF. Approximately 70% of the tagging was done by commercial fishermen trained in tagging procedures, the rest by NMFS technicians. Single Floy[4] spaghetti-dart tags were inserted on the left side below the second dorsal fin with the aid of a beveled stainless steel tube so that the tag barb was lodged in the pterygiophores of the fin. Only fish judged to be in very good condition were tagged; fish hooked in the roof of the mouth or showing signs of extreme exhaustion or severe bleeding were rejected. For each tagged fish a record was kept on 1) tag number, 2) date and time of release, 3) fork length at time of release, 4) condition at tagging, and 5) longitude and latitude of release. Additional tagging details are given in Laurs et al. (1976).

Recovery Procedures

Recoveries were made by sport and commercial fishermen, unloaders, and cannery workers. Information was obtained on 1) tag number, 2) date of recapture, 3) fork length at time of recovery, and 4) longitude and latitude of recapture. Most recapture locations were given as loran coordinates, which were converted to longitude and latitude, but the recapture locations for tags recovered by unloaders and cannery workers were often reported inexactly, e.g., as "off central California." Direct measurements of fork length were available for about one-half the fish recovered. For most of the remainder only the weight at recovery was given, and fork length was estimated using Clemens' (1961) weight-length relation. Observed fork lengths were measured to the nearest centimeter. Bias in estimating fork length from observed weight using the inverted weight-length relationship was judged to be <0.5 cm in absolute value over the length range represented in the recapture sample, so subsequent growth analyses were based on the combined sets of observed and estimated lengths.

Data Screening

The tag return data were screened to exclude cases where information was incomplete, unreliable, or clearly inaccurate. Out of 741 tag returns made from 1971 through 1978, 305 were rejected (Table 1). In 15 cases length at release was not measured, in 116 cases the recapture date was unknown, and in 68 cases neither length nor weight was measured at recovery. In 79 other rejected cases the length at recovery was not measured and the weight only guessed without the use of scales. Additionally, in 27 instances a gross error was apparent in the measurement of fork length either at release or recovery.

The final accepted data set of 436 cases includes observations on 28 albacore showing negative estimated growth. We assume these are a result solely of measurement error or error in estimation in cases where the recovery weight was converted to length, and we assume such error occurs throughout the data set independently of size or time between release and recapture (time out).

One of the common steps in screening tag recovery data for growth studies is to partition the data according to length at release, compute linear regressions of growth increment on time out within each subset, and then reject rare observations, usually those departing from expectations by more than two standard deviations (Schaefer et al. 1961; Joseph and Calkins 1969). We abandoned this step because the number of

[4]Mention of a commercial company or product does not constitute an endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of number of tagged fish released, recovered, rejected, and accepted for analysis of albacore growth.

Year	No. tagged fish released	No. tagged fish recovered	Rejected tag recoveries (no.)						No. tag recoveries accepted for analysis
			Missing release length	Missing recapture date	Missing recovery size	Weight at recovery estimated	Measurement error	Total	
1971	887	34	2	6	5	1	0	14	20
1972	1,557	132	1	23	13	16	10	63	69
1973	1,805	111	0	23	10	12	2	47	64
1974	2,486	175	4	22	16	22	8	72	103
1975	1,349	115	1	17	13	15	2	48	67
1976	1,581	85	0	15	8	10	3	36	49
1977	1,221	25	0	4	0	3	0	7	18
1978	2,719	58	1	6	3	0	2	12	46
Unknown	—	6	6	—	—	—	—	6	0
Total	13,605	741	15	116	68	79	27	305	436

"outliers" it identified was consistent with the number expected due to chance alone, because the procedure has no sensible stopping rule, and because even with length at release fixed, the expected relationship between growth increment and time out is nonlinear.

Grouping of Data

The selected data were cross-classified by location of tagging and location of recapture (Table 2). Nearly 66% of the 436 tagged fish were released inshore,[5] and of these 74% were released south of lat. 40° N, the remainder north of this latitude. Eighty-four percent of recaptured fish released inshore south of lat. 40° N were recovered in the same area, 5% were recovered inshore north of lat. 40° N, 1.4% were taken in the offshore area east of long. 180°, and 8.4% were recovered in the western Pacific. Of the recovered fish tagged and released inshore north of lat. 40° N, only 8.2% were recaptured inshore south of lat. 40° N, 1.4% were taken east of long. 180° in the offshore area, 27.4% were recovered in the area of tagging and 63% were recovered in the western Pacific. Of the recovered fish tagged offshore, 70.5% were recaptured either inshore north of lat. 40° N or west of long. 180°, and only 27.5% were recovered in the southern inshore area.

For purposes of constructing and testing hypotheses about differences in growth rates, tag returns were grouped into three categories depending on recapture location: 1) Group A includes all fish recaptured inshore south of lat. 40° N, except those released inshore north of lat. 40° N (221 fish). 2) Group B consists of tag recoveries made inshore north of lat. 40° N, excluding those released inshore south of lat. 40° N (75 fish). 3) Group C consists of all tag recoveries made west of the 180° meridian (114 fish). The three groups together comprise 410 recaptures. Excluded are 6 fish tagged inshore north of lat. 40° N and recovered south of this line the following year or later; 11 fish released south of lat. 40° N and recaptured in the northern inshore area (1 the same season, 10 in following years); 6 fish recaptured offshore east of long 180°; and 3 fish whose recapture locations are unknown.

[5]Fish released (recaptured) east of long. 130° W in the area south of lat. 49° N, or east of long. 135° W between lat. 49° and 54° N were considered to be released (recaptured) inshore. Demarcation of the inshore area boundary is based on analysis of tag recoveries discussed in Laurs and Lynn (1977).

TABLE 2.—Classification of selected tag data by locations of release and recapture.

	Release location				
	Inshore[1]—from lat. 40° N				
Recapture location	South	North	Total	Off-shore	Grand total
East of long. 180°	194	27	221	98	319
Inshore[1]	191	26	217	96	313
South of lat. 40° N	180	6	186	41	227
North of lat. 40° N	11	20	31	55	86
Offshore	3	1	4	2	6
West of long. 180°	18	46	64	50	114
Unknown	2	0	2	1	3
Grand total	214	73	287	149	436

[1]See text footnote 5.

Growth Models

We used observations of growth increment, length at tagging, and time at liberty to estimate the growth rate, K, and the asymptotic length, L_∞, of the standard deterministic von Bertalanffy model. In addition, we considered an extension of the von Bertalanffy model which allows the growth rate to vary with age in a simple manner. In general terms, we assumed that the expected growth increment for the jth fish in the ith group ($i = 1,\ldots, m$; $j = 1, 2,\ldots, n_i$), given the initial length and time out, could be stated as

$$E(\Delta L_{ij}) = \int_{t_{ij}}^{t_{ij}+\Delta_{ij}} G(u)\,(L_\infty - L(u))\,du,$$

where $E(\Delta L_{ij})$ = expected growth increment of jth tagged fish in ith group during $(t_{ij}, t_{ij} + \Delta_{ij})$
$= L(t_{ij} + \Delta_{ij}) - L(t_{ij})$
t_{ij} = age of jth fish in ith group at time of release
Δ_{ij} = time at liberty for jth fish in ith group
$L(u)$ = length at age u
L_∞ = asymptotic length
$G(u)$ = unspecified age-dependent growth rate.

If we set $G(u) = K$ = constant, we have the standard von Bertalanffy model, and

$$E(\Delta L_{ij}) = (L_\infty - L_{1_{ij}})\,[1 - \exp(-K\Delta_{ij})],$$

where $L_{1_{ij}} = L(t_{ij})$.

We call this Model 1. (We omit subscripts on

parameters, even though group-specific parameters are implied.)

In Model 1 we assume that the ratio of instantaneous growth rate, $dL(u)/du$, to potential growth, $L_\infty - L(u)$, is K, a constant. Instead, we may suppose generally that this ratio varies with age. We considered one such situation. In this model, Model 2, we assume that stresses due to capture, handling, and tagging will initially reduce the growth rate of a tagged fish below its usual level, but that as time passes the normal growth process will be restored. Specifically, in our analysis of Model 2 we assume the standard model holds for untagged fish but that when a fish is tagged its normal growth pattern is interrupted, such that

$$G(u) = K, \qquad 0 < u < t_{ij}$$
$$G(u) = K/\left\{1 + \alpha \exp[-\beta(u - t_{ij})]\right\} \qquad t_{ij} \leq u.$$

We assume $K \geq 0$, $\beta > 0$, and $\alpha \geq 0$. Model 2 says that following tagging the growth rate is immediately reduced to a fraction $(1 + \alpha)^{-1}$ of its normal value, K, and then returns to K asymptotically (Figure 1). L_∞ is assumed to be unaffected.

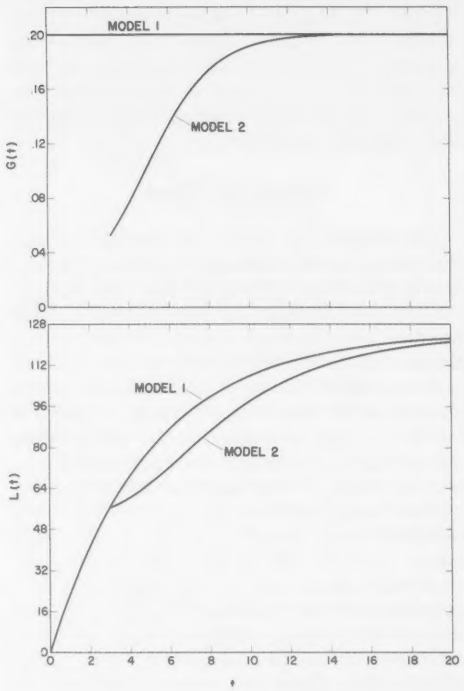

FIGURE 1.—Standard von Bertalanffy growth model (Model 1), and an extension (Model 2) incorporating a temporary reduction in growth rate, $G(t)$, following tagging. The resulting growth pattern, $L(t)$, is altered. Time units are arbitrary.

Parameter Estimation

In the standard von Bertalanffy model as applied to tag recapture data, there are two parameters to be estimated, K and L_∞. The usual approach is to estimate them simultaneously, and we did so using the FORTRAN program BGC 4 written by Tomlinson (1971). This routine finds $\hat{K}$ and $\hat{L}_\infty$ as those parameter values which minimize

$$S = \sum_{j=1}^{n_i} \left\{ L_{2_{ij}} - [L_\infty - (L_\infty - L_{1_{ij}}) \exp(-K\Delta_{ij})] \right\}^2,$$

where $L_{2_{ij}} = L(t_{ij} + \Delta_{ij})$. Since $E(L_{2_{ij}})$ is a nonlinear function of K, parameter estimates derived using this procedure are prone to serious bias unless observations on $L_{2_{ij}}$ are made over a wide range of $L_{1_{ij}}$ and Δ_{ij}. Presumably, it is also desirable that they be made uniformly in the plane of these two variables.

The parameters of Model 2 may also be estimated jointly using nonlinear least squares methods, but estimates of L_∞ and correlated parameters suffer the same drawbacks as estimates of the standard von Bertalanffy model parameters derived from BGC 4

An alternative approach in fitting both models is to estimate L_∞ and the other parameters sequentially. Where the oldest members of the population have been intensively sampled and an upper asymptote to length is clearly demonstrated in the data, a reasonable estimate of L_∞ is the length of the largest fish seen in the catches, or the average length of the largest specimens observed. Which estimator to use depends on one's conceptual model of the growth process—L_∞ can be regarded as the mean of a distribution of asymptotic lengths in the population, or strictly as an upper bound to the length any fish in the population can achieve. With the value of

L_∞ determined, the other parameters may be estimated by the least squares method using the general model:

$$Y_{ij} = -\ln\left(\frac{L_\infty - L_{2_{ij}}}{L_\infty - L_{1_{ij}}}\right) = \int_{t_{ij}}^{t_{ij}+\Delta_{ij}} G(u)\,du + \epsilon_{ij},$$

where we assume that ϵ_{ij} are independent errors with zero means and variances σ^2_{ij}.

This approach handily accommodates any well-behaved form of $G(u)$. In the case of Model 1, the problem of estimating K reduces to a simple linear regression:

$$Y_{ij} = K\Delta_{ij} + \epsilon_{ij}. \quad (1)$$

When a reasonably accurate estimate of L_∞ can be made by sampling the catches, this sequential estimation procedure for Model 1 has the advantage that the range of observations on $L_{1_{ij}}$ and Δ_{ij} is not so critical.

With Model 2, the sequential method may be applied to estimate K, α, and β using the equation:

$$Y_{ij} = K\Delta_{ij} - \left(\frac{K}{\beta}\right)\ln\left\{(1+\alpha)/[1+\alpha\exp(-\beta\Delta_{ij})]\right\} + \epsilon_{ij}. \quad (2)$$

The desirability of fitting this nonlinear model to any particular set of data may be judged by examining the residuals around the least squares fit of Model 1 (Equation (1)). As is evident from Figure 2, the detection of nonlinearity in this manner requires that observations be available uniformly over a broad range of Δ_{ij}.

Covariance Analysis

One of our chief objectives was to determine whether growth rates differed between groups of fish, based on estimates of parameters of the standard von Bertalanffy model. Since BGC 4 estimates of K and L_∞ are highly correlated, particularly when few large fish are in the sample, and since probability statements concerning intergroup comparisons of both K and L_∞ were not possible, we used the sequential estimation procedure. For the ith group of fish we assumed

$$E(Y_{ij}) = K_i\,\Delta_{ij}, \quad (3)$$

where $Y_{ij} = -\ln\left(\frac{L_\infty - L_{2_{ij}}}{L_\infty - L_{1_{ij}}}\right)$

and specified a fixed value for L_∞. Then we developed and applied a weighted zero-intercept covariance analysis to test hypotheses of the form:

$$H: K_1 = K_2 = \ldots = K$$

on the basis of F-statistics. Statistical weights were computed on the assumption that $\sigma^2_{ij} \sim \Delta_{ij}$, as suggested by Figure 2.

RESULTS

Standard Model

Joint estimates of K and L_∞ for Groups A, B, and C, based on the BGC 4 program, are shown in Table 3. We consider the estimates inaccurate, owing to sampling biases discussed earlier. In particular, we think the unexpectedly low L_∞ estimates (and correspondingly high K estimates) are due to the absence of very large albacore in the release and recovery samples. Of the 410 selected tag returns, 141 exceeded 80 cm fork length at recapture, but only 42 were >85 cm and just 11 were >90 cm. The average fork length of tagged albacore at time of release was 63.7 cm (range 45-89 cm), and at recovery, 75.7 cm (range 51-103 cm).

Because of the difficulties with BGC 4 estimates, we based intergroup comparisons on estimates of K from the sequential estimation procedure. A preliminary F-test showed no significant difference in K between fish whose lengths at recovery were measured and those whose lengths were estimated from the inverted weight-length relationship. Further sequential analyses (as well as the earlier BGC 4 estimates) were therefore based on all data, regardless of how recovery length was determined.

L_∞ was fixed at 125 cm, a reasonable choice well supported by available length-frequency data. Although Otsu and Sumida (1970) reported an albacore measuring 132.7 cm from the

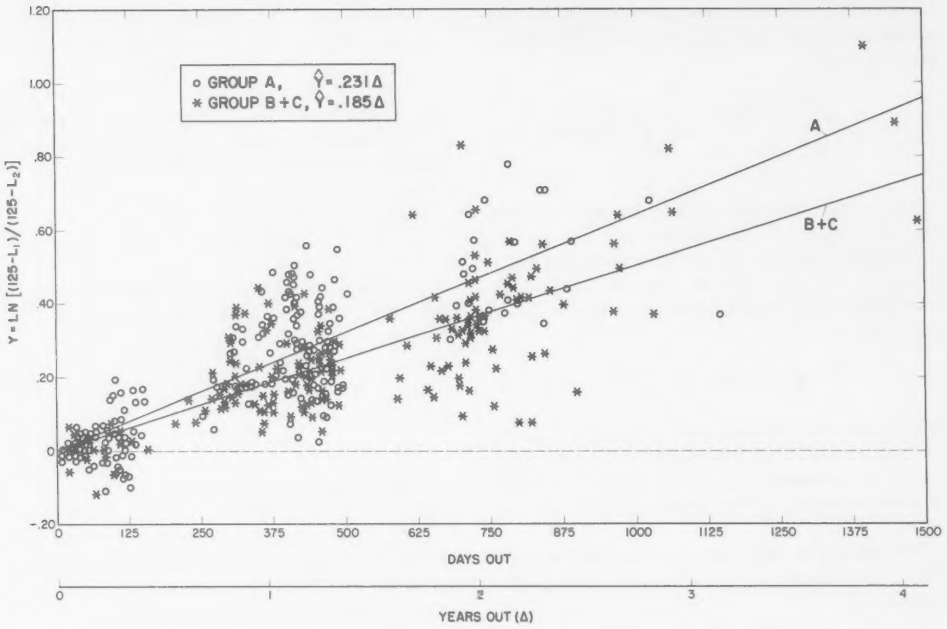

FIGURE 2.—Regression of growth variable, Y, on years between release and recapture for albacore of Groups A (221 fish) and B + C (189 fish). The slopes are estimates of the von Bertalanffy growth parameter, K, and they are significantly different.

TABLE 3.—Estimates of von Bertalanffy growth parameters for North Pacific albacore by recapture group and estimation method, assuming stock boundary at lat. 40° N.

Recapture group	Sample size	BGC4 estimates		Sequential estimates		Average time out Δ (d)
		$\hat{L}_\infty$ (cm)	$\hat{K}$ (yr^{-1})	Fixed L_∞ (cm)	$\hat{K}$ (yr^{-1})	
A	221	94.5	0.505	125.0	0.231	313
B	75	107.5	.272	125.0	.193	400
C	114	98.5	.345	125.0	.184	588
B + C	189	102.1	.310	125.0	.185	513
A + B + C	410	100.9	.342	125.0	.199	405

Hawaiian longline fishery, which harvests the largest North Pacific albacore known, specimens >125 cm are extremely rare. With L_∞ fixed at 125 cm, Group A had the highest growth rate estimate, $\hat{K}_A = 0.231$/yr (Table 3). Group B and $\hat{K}_B = 0.193$, and Group C had the lowest growth rate estimate, $\hat{K}_C = 0.184$. When Groups B and C were pooled into a "North" category, the resulting $\hat{K}_N$ was 0.185. The estimate of K for all three groups combined was 0.199.

Table 3 also shows the statistics on average time between release and recapture. Group A fish were at liberty an average of 313 d, while Group B fish were out 400 d, and Group C fish, 588 d. Tagged fish from Groups B and C combined were at large an average of 513 d.

The estimates suggest that the North fish, Groups B and C, had a lower growth rate than the South fish of Group A. Such a difference might arise if, as we suppose, the North fish budget more of their available energy for migration compared with the South fish, and relatively less energy for growth. Tag release and recovery results indicate that the North fish make longer migrations, traveling between coastal waters off the United States Pacific Northwest and coastal waters off Japan, while the South fish undertake shorter migrations between coastal waters south of Cape

Mendocino, Calif., and the central North Pacific east of 180° (Laurs[6]).

The hypothesis of equal growth rates was tested using the weighted zero-intercept analysis of covariance, and was rejected at the 0.5% significance level (Table 4, Figure 2). In pairwise comparisons between individual groups, the only nonsignificant difference in growth rate was between Groups B and C.

Are the observed differences in growth rates of tagged albacore consistent with other information? To check this, we examined the length composition of albacore catches along the U.S. west coast (Figure 3). The length-frequency plot for catches north of lat. 38° N during the period when most recaptures were made, 1972-78, showed modes at about 64 and 76 cm and a hint of one at 54 cm. Catches south of lat. 38° N showed the 54 cm mode, but had primary modes at about 66 and 79 cm. The discrepancy between modes of the older albacore is further evidence of a slower growth rate for North fish, assuming these modes represent fish of the same age. To see if length-frequency data and tag data agreed, we computed the expected fork lengths under each $\hat{K}$ at annual time steps and compared these with observed modes in the length-frequency distributions. Starting with some initial fork length, L_1, we used the equation $L_i = a + bL_{i-1}$, $i = 2, 3, \ldots$, where $a = L_\infty (1 - \exp(-K))$ and $b = \exp(-K)$. Setting $L_1 = 54$ and $L_\infty = 125$ cm, we found the sequence of lengths 54.0, 66.0, and 76.0 cm for the North group albacore; and 54.0, 68.6, and 80.3 cm for the South fish. These are reasonably consistent with the observed sequences of length modes.

Extended Model

Plots of residuals from the standard model against days out (Figure 4) showed a tendency toward negative deviations during the first several months after tagging, suggesting that some of the residual variation could be attributed to "lack of fit" (Draper and Smith 1966). For example, of the 221 recaptures analyzed in Group A, 90 were taken within 6 mo of tagging, and 70% of the Model 1 residuals corresponding to these early recaptures were negative. We therefore fit Model 2 to each set of data, using the sequential estimation procedure (Equation (2)) with $L_\infty = 125$ cm. Resulting estimates of K were 3-6% larger than the corresponding estimates from the standard linear model; thus, if Model 2 is correct, systematic bias in the latter estimates does not appear to be serious.

However, estimates of α and β were relatively large in all cases, suggesting that the growth rate may drop abruptly to near zero immediately after

[6]Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-79-17, 10 p.

TABLE 4.—Analysis of covariance comparing growth rate of Group A North Pacific albacore with growth rate of Group (B + C) albacore, assuming stock boundary at lat. 40° N. Probability of obtaining F statistic this large under null hypothesis is <0.005.

Source of variation	df	Residual SS	MS	F
Individual lines:				
A	220	1.1476		
B + C	188	1.7362		
Pooled	408	2.8837	0.0071	
Common line	409	3.1009		
Difference	1	.2172	.2172	30.72

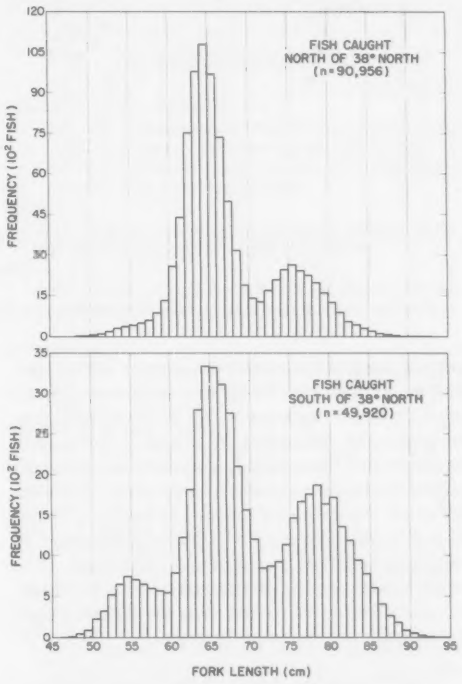

FIGURE 3.—Composite length-frequency distributions for North Pacific albacore caught north of lat. 38° N and south of lat. 38° N off the U.S. west coast during the 1972-78 fishing seasons.

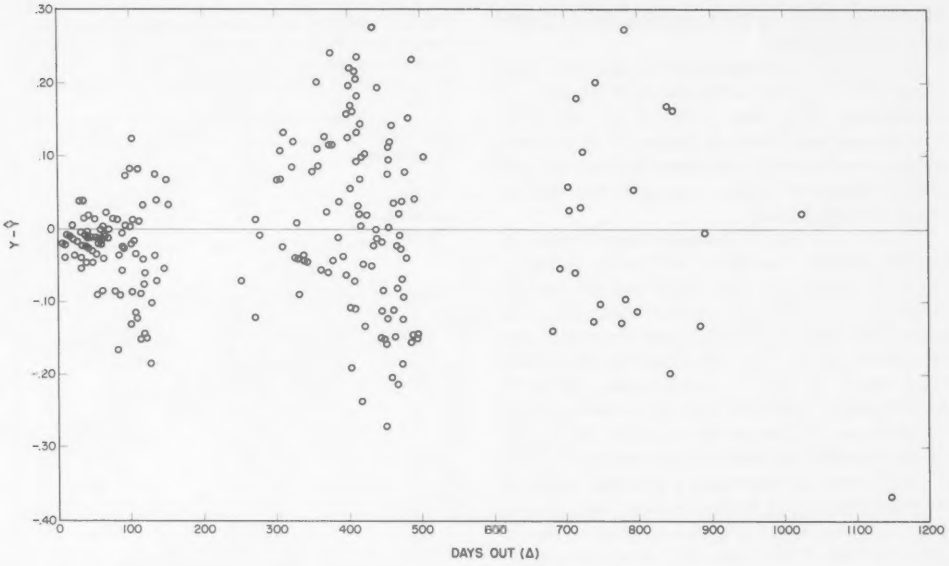

FIGURE 4.—Residuals from the fit of Model 1 to the Group A albacore data, as a function of days out.

tagging and then recover to normal within the first year of liberty. While this basic response to tagging stress appears to be a reasonable hypothesis, the estimates of α and β were very unstable and little confidence could be placed on projected growth rate recovery patterns. Further, although the extended model fits the data better than the ordinary von Bertalanffy in the sense of reducing residual variation, as expected, this improvement is only slight; considering the high variance displayed in the data we do not reject the simpler von Bertalanffy model.

DISCUSSION AND CONCLUSIONS

The results of our growth analysis are strengthened by their consistency with other findings, but the assumptions of our analysis need to be tested. In particular, we assumed that our estimate of L_∞, 125 cm, was the same for all groups of North Pacific albacore. If $L_\infty(B + C) > L_\infty(A)$, our conclusions concerning differences in growth rate are reinforced. But if the South fish, Group A, actually tend toward a larger asymptote in fork length than the North fish of Groups B and C (there is no evidence of this), then the differences between estimates of K might not be significant. For example, if we assume $L_\infty(A) = 130$ cm and $L_\infty(B + C) = 120$ cm, the differences vanish. More to the point, unless the L_∞'s are the same, the comparison of growth rates between groups is no longer conveniently reduced to a comparison of K estimates. When the assumption of equal L_∞ is valid, the actual value of L_∞ assumed is relatively unimportant as far as the covariance analysis is concerned; our conclusions were the same when L_∞ was fixed at 120, 130, and 135 cm.

In Model 1, the standard von Bertalanffy model, we also assumed that the growth rate was unaltered by the presence of the tag or by the stress imposed in its application. In our analysis of Model 2 we explored the question of whether tagging might have affected growth rate in a specified way, and Model 2 fits our data only slightly better than Model 1. However, effects of the sort we hypothesized might easily be masked by high variance in the data. Nevertheless, if the effect of tagging were simply to reduce the normal growth rate, K, suddenly and permanently to a lower level, K', it would go undetected by our analysis. To determine the validity of the tag-effect assumption, we need to compare the growth rates of tagged fish with those of untagged, "control" fish.

Such a comparison was recently made for bait-boat-caught southern bluefin tuna, *T. maccoyii*, by Hearn,[7] who found that fish caught 3 wk after being tagged weighed 14% less than untagged fish of the same length in the same schools. Assuming the tagged bluefin tuna also grew less in length than their untagged counterparts, this 14% weight loss would be an underestimate. At any rate, after 1 yr at liberty no difference in weight was discernible.

We found that the growth rate of North Pacific albacore recaptured either off the coast of North America north of lat. 40° N or in the western North Pacific off Japan was significantly lower than for tagged albacore recaptured off North America south of lat. 40° N during 1972-78. The differences in growth rate of tagged fish are remarkably consistent with differences in length-frequency distributions of albacore caught off North America north and south of lat. 38° N during the period when most recaptures were made. These findings add to a growing body of evidence (Brock 1943; Laurs and Lynn 1977; Laurs et al.[8]; Laurs and Lynn[9]) that North Pacific albacore are not as homogeneous as usually assumed, and that there may be at least two subgroups of albacore: one which supported the Japanese pole-and-line fishery and the United States and Canadian fisheries in waters north of about lat. 40° N from 1972 to 1978, and another which did not contribute significantly to the Japanese surface fishery, but supported the United States coastal fishery south of lat. 40° N during this period. If such a distinction is valid, the situation is surely more complex and dynamic than we have supposed, with each stock's contribution to each fishery varying from year to year. Presumably such variation would be tied directly to changes in oceanographic conditions. And undoubtedly the latitudinal boundary was not fixed exactly at lat. 40° N during 1972-78, as we assumed, but analyses based on assumed boundaries at lat. 38° and 42° N gave the same results. If an accurate assignment of tagged fish to stock were possible, a more powerful test of growth differences could be made.

A finding that more than one subpopulation or stock is involved in the North Pacific albacore fisheries would have important consequences, of course, both for stock assessment, fishery evaluation and management policy analysis, and for development of accurate catch forecasting systems. It is important that further work be done to identify stocks, and to elucidate their origins, migratory habits, and degree of interchange.

[7]Hearn, W. S. 1979. Growth of southern bluefin tuna (*Thunnus maccoyii*). Commonwealth Scientific and Industrial Research Organization, Division of Fisheries and Oceanography, Cronulla, New South Wales, Australia, Unpubl. manuscr.

[8]Laurs, R. M., R. J. Lynn, and R. N. Nishimoto. 1975. Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1975. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-75-84, 49 p.

[9]Laurs, R. M., and R. J. Lynn. 1976. Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1976. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-36, 51 p.

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ECONOMIC FEASIBILITY OF DOMESTIC GROUNDFISH HARVEST FROM WESTERN ALASKA WATERS: A COMPARISON OF VESSEL TYPES, FISHING STRATEGIES, AND PROCESSOR LOCATIONS

C. M. LYNDE[1]

ABSTRACT

An economic model relating fishing costs to vessel characteristics and operating conditions was used to estimate the costs and benefits to U.S. fishermen of harvesting groundfish under a variety of conditions. Comparisons were made between 1) two vessel types, 2) two modes of operation: delivering to a floating processor and delivering to a shore-based processor, and 3) three fishing strategies in Alaskan waters.

Fishing costs were about 50% less and fuel efficiency was 28% higher for the smaller of the two vessels. Costs for either vessel decreased by 30% and fuel efficiencies increased by 35% when delivering the catch to a floating processor rather than delivering to port. Cost estimates for both sea delivery and port delivery were sensitive to changes in fuel price. A $0.026/l ($0.10/gallon) increase in fuel price increased the break-even ex-vessel prices by $6/t for sea delivery and $8/t for port delivery in one example.

Given the ex-vessel prices currently offered by two joint venture firms and a fuel price of $0.277/l ($1.05/gallon), break-even catch rates were calculated for each vessel type and targeting strategy, assuming sea delivery. All of the catch rates were considered highly feasible when compared with the average catch rates of foreign trawlers and experimental U.S. fisheries in the area. Assuming similar prices were offered by shore-based processors, the break-even catch rates, although higher than under the sea delivery mode, were still considered feasible. However, the margin for profit is narrower and could be negative with increases in fuel price.

Since the implementation of the U.S. 200 mi economic zone (public law 94-265, 13 April 1976), a great deal of interest has been generated by the large stocks of groundfish off the western Alaska coast. The combined annual optimum yield of walleye pollock, *Theragra chalcogramma*; Pacific cod, *Gadus macrocephalus*; sablefish, *Anoplopoma fimbria*; flatfish, and rockfish from the eastern Bering Sea, Aleutians, and western Gulf of Alaska (Kodiak Island westward; Figure 1) has been estimated to be over 1.6 million t (North Pacific Fisheries Management Council 1978a, b). In perspective, this potential is equivalent to 58% of the total 1978 U.S. commercial landings of all species from all areas (U.S. Department of Commerce 1979). Although the Fisheries Conservation and Management Act of 1976 grants preference to U.S. harvesters over foreign fishing fleets, a domestic trawl fishery for groundfish has been slow to develop, and the precise set of conditions necessary to stimulate growth has been a topic of considerable concern (Sullivan and Heggelund 1979; Gorham[2]; Little[3]; Alaska Fisheries Development Foundation[4]; Combs[5]).

In this paper I demonstrate the utility of an economic model which estimates fishing costs based on vessel characteristics and operating conditions. The model is used to predict the fishing costs and the catch rates required to cover costs under conditions that are likely to occur during future domestic groundfish harvests from western Alaska. These catch rates are then compared with actual catch rates observed in foreign and experimental domestic fisheries in the area. In this way I seek to contribute to the development of an appropriate methodology for evaluating the economic feasibility of domestic groundfishery expansion in Alaska.

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Manuscript accepted November 1980.
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[2]Gorham, A. H. 1978. Interim report on an investigation of joint U.S./foreign ventures in the developing commercial fishery off Alaska, 12 p. Submitted to the North Pacific Fishery Management Council.

[3]Little, A. D. 1978. The development of a bottomfish industry: Strategies for the State of Alaska, vol. 1, 33 p.

[4]Alaska Fisheries Development Foundation. 1978. Development proposal for bottomfish off Alaska, 37 p.

[5]Combs, E. R. 1979. Prospectus for development of the United States fisheries. Alaska groundfish, p. 25-112, 327-362. Prepared for Fisheries Development Task Force, NMFS, NOAA.

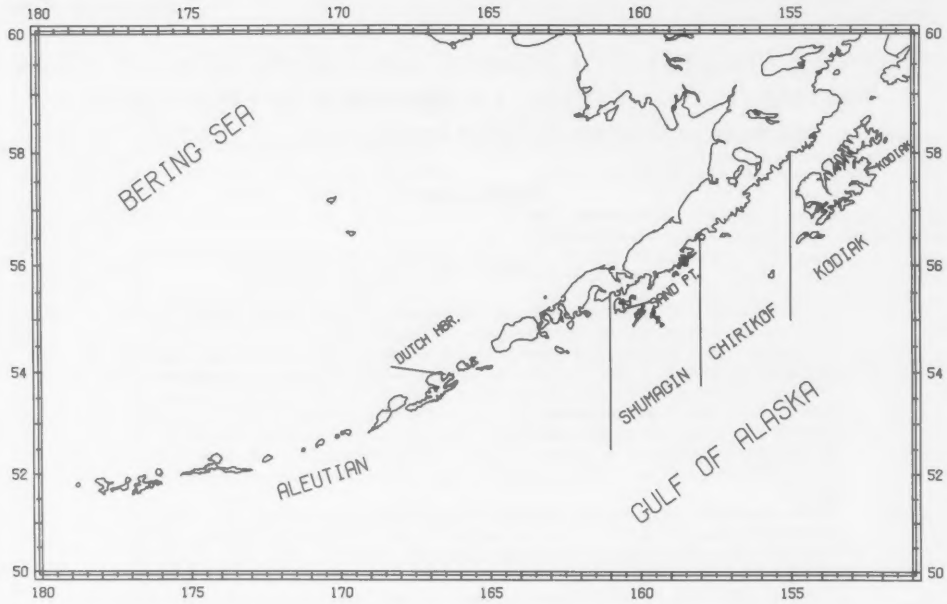

FIGURE 1.—Western Gulf of Alaska and eastern Bering Sea and selected International North Pacific Fisheries Commission areas.

In addition, an economic model such as the one described in this paper may be helpful to fishermen considering future diversification. The model could be easily adapted for use with a programmable calculator or onboard microcomputer. After tailoring the parameters to his vessel, the vessel owner need only key in a few pertinent variables such as expected ex-vessel price, distance to the fishing ground, and fuel price and receive an immediate estimate of the average catch rate required to cover his expenses.

One advantage of the modeling approach is that it allows one to examine the effects of individual factors of interest by allowing these factors to vary while holding all others constant. This paper examines the effects upon fishing costs and fuel efficiency (fish harvested per fuel consumed) of the following factors: vessel type, processor location, fishing strategy, and fuel price. Costs and benefits are estimated only within the harvesting sector. A consideration of economic feasibility within the processing and marketing sectors of the industry is beyond the scope of this paper.

THE ECONOMIC MODEL

Given a set of operating conditions, such as distance to the fishing grounds and number of crew required, a set of vessel characteristics, such as cruising speed and hold capacity, as well as a schedule of capital expenses, such as the vessel's initial value and finance rate, the model projects the costs of a single fishing trip and computes a set of catch rates and corresponding ex-vessel prices required to balance fishing costs with net revenue.

Assuming the crew (including skipper) receives shares of the revenue as remuneration, the benefit (B_{ij}) to the vessel owner of a single fishing trip is simply:

$$B_{ij} = (1 - S_{ij}) \cdot U \cdot P$$

where S_{ij} = total crew shares (expressed as decimal fraction) for the ith vessel type and jth mode of operation, U = total catch, and P = ex-vessel price.

Fishing costs are commonly categorized as fixed

or variable. Fixed annual costs are invariate with respect to the amount of vessel use per year. Using the subscripts i and j as before, the fixed annual costs can be prorated over the length of the fishing trip, allowing for yearly down time due to bad weather, maintenance, and vacations, according to the formula:

$$F_{ij} = [T_{ij}/(365 - D_i)]A_i$$

where F_{ij} = fixed costs per trip, T_{ij} = length of trip in days, D_i = total inoperative days per year, and A_i = annual fixed costs.

Assuming the crew pays a share of certain variable costs, the total fishing costs (C_{ij}) incurred by the vessel owner per trip can be expressed as:

$$C_{ij} = F_{ij} + V_{ij} + (1 - S_{ij})W_{ij}$$

where V_{ij} = variable costs incurred only by vessel owner and W_{ij} = variable costs incurred by owner and crew.

Setting benefits equal to costs and solving for ex-vessel price gives:

$$P = \left[\frac{F_{ij} + V_{ij}}{1 - S_{ij}} + W_{ij}\right] \frac{1}{U} . \qquad (1)$$

This equation defines the ex-vessel price, P, required to break even for a fishing trip with catch rate U. Conversely, Equation (1) can be used to compute the catch rate required to break even for a fishing trip when the ex-vessel price is P. A computer program (TRAWL)[6] was written to calculate solutions for P over a range of catch rates for a given vessel type and mode of operation.

A tacit assumption has been made that the criterion for economic feasibility of a fishery is met if a fisherman can receive enough revenue to balance the variable and fixed costs of fishing. In fact, if the vessel and gear already exist and no other more profitable fisheries are available, it will be economically advantageous for the fisherman to enter the fishery in question if it provides enough revenue to cover variable costs alone, since the fixed costs will be incurred whether fishing or not. However, the objective of this paper is to examine the conditions under which the fisherman can cover both fixed and variable costs.

The model relies on a number of assumptions which relate fishing costs to the vessel type and the mode of operation. Table 1 lists these assumptions according to a cost accounting format similar to that suggested by Smith (1975). A description of the cost derivations and the sources of their estimates can be found in Appendix I. Note that, unlike Smith's cost accounting procedures, the average annual cost of financing is included here as a fixed cost. Variable costs IIB-D (Table 1), represented in total by symbol W_{ij} in the above development, are commonly deducted from the gross revenue before the crew shares are taken. Fixed costs IA-F and variable costs IIA are in turn represented by symbols A_i and V_{ij} above. Crew

[6]Written in Fortran IV. A program listing and user's guide are available from the author on request.

TABLE 1.—Fixed and variable fishing costs as a function of vessel characteristics and operating conditions.

Cost category	Parameter values and variables
I. Fixed annual costs:	
A. Routine boat and engine maintenance	\$0.07 × vessel's initial value (VIV)
B. Insurance:	
1. Hull	0.021 × VIV
2. P & I	2,100.0 × no. in crew
C. Depreciation	0.0533 × VIV
D. Association dues	2,500.0
E. Contingencies/miscellaneous	0.05 × (above total)
F. Average annual finance cost	$1.0 \times \text{VIV} \times \left[\frac{\%\ \text{financed}}{\text{yr financed}}\right] \times \left[\frac{ni\,(1+i)^n}{(1+i)^n - 1} - 1\right]$
n = no. of payment periods	
i = interest rate per period	
II. Variable costs:	
A. Fishing gear repair and replacement (see Append. I)	\$1.0 × gear costs/h × towing h
B. Fuel:	
1. Cruising	0.2105 × horsepower × travel h × fuel price/l
2. Towing	0.1579 × horsepower × towing h × fuel price/l
3. Stove and auxiliaries	30.283 × trip h × fuel price/l
4. Lube oil	0.235 × trip h × price/l
C. Food	13.50 × trip d × no. in crew
D. Ice	$25.00 \times \frac{\text{capacity for groundfish (wt)}}{1 + (\text{fish:ice wt ratio})}$

shares, composing S_{ij}, are assumed to be 12% for the skipper and 7% for each additional crew member.

FACTORS OF INTEREST

Vessel Types

Two representative vessel types were considered: a 33 m (108 ft) combination crabber/trawler and a 25-28 m (80-92 ft) bottom trawler or combination shrimp and groundfish trawler. These vessel types are thought to be representative of many of the U.S. vessels likely to participate in future western Alaska groundfish harvests.

The vessel characteristics and capital expenses for the two vessel types are listed in Table 2. The vessel characteristics are based on statistical analyses of vessels registered with the State of Alaska as performed by Katz et al.[7] The characteristics of vessel type 1 are average values for a group of combination crabber/trawler vessels fishing for king and tanner crab in Alaska (class 8.5 of Katz et al. (footnote 7)). Similarly, the characteristics of vessel type 2 are representative of a group of Alaska shrimp trawlers and smaller crabber/trawlers (class 8.3 of Katz et al.). Type 2 vessel characteristics are also believed to be representative of the larger groundfish trawlers of California, Oregon, and Washington. The capital expenses incurred by owners of these vessel types were estimated with the help of industry personnel (Pigott[8]; Jaeger[9]).

TABLE 2.—Vessel characteristics and capital expenses for two representative vessel types (see text).

Item	Vessel type 1	Vessel type 2
Vessel characteristics:		
Age, yr	1-2	5
Keel length, m (ft)	33 (108)	25-28 (80-92)
Engine type	Diesel	Diesel
Horsepower	1,000	650
Cruising speed, kn/h	11.5	10.0
Hold volume, m^3 (ft^3)	225 (8,000)	140 (5,000)
Capacity for groundfish, t	150	115
Capital expenses:		
Vessel's initial value, $	1,500,000	500,000
Amount financed, %	80	80
Annual finance rate, %	10	8.5
Amortization, yr	20	15
Payment period	Monthly	Monthly
Interest per period (i), %	0.7174	0.6821
No. of payment periods (n)	240	180

Processor Location and Mode of Operation

Two modes of operation were compared: delivering the catch at sea to a floating processor and delivering the catch to a land-based processor. The method of sea delivery is currently being employed by U.S. fishermen participating in two international joint fishing ventures for groundfish off the western Alaska coast. Under the arrangements of these joint ventures, the U.S. trawlers transfer their catch at sea via detachable cod ends to large floating processors provided by the foreign partner. The fish are then processed aboard the factoryships and the resulting product is taken to foreign ports and sold on the foreign market.

During the sea delivery mode of operation, it is assumed that: 1) the floating processor is on or near the fishing grounds, 2) fishing vessels have at least two cod ends so replacement after each haul is not delayed, 3) full cod ends are towed to the processor and empty cod ends are returned to the fishing vessel periodically by a motor launch, and 4) the processing rate of the factory vessel is not limiting.

Table 3 lists the estimated operating conditions for the sea delivery and land delivery modes of operation. Differences between the two modes are as follows:

TABLE 3.—Operating conditions for vessels harvesting groundfish from western Alaska. Delivering the catch at sea versus delivering to a land-based processor.

Item	Mode of operation: Sea delivery	Land delivery
No. of crew required (including captain)	4	5
Maximum trip length:		
Vessel type 1	28	7
Vessel type 2	26	7
Fish:ice weight ratio (if applicable)	N.A.	2:1
Search time per trip, h	6	6
Towing time per day on grounds, h	9	9
Time spent in port replenishing supplies, refueling, and unloading	24	24
Distance to fishing grounds:		
Gulf of Alaska	75	75
Bering Sea:		
Walleye pollock or Pacific cod	65	65
Sole species	220	220
Gear costs per hour of towing:		
Vessel type 1	20.57	20.57
Vessel type 2	16.90	16.90

[7]Katz, P. L., K. C. Lee, L. J. Bledsoe, and J. Buss. 1976. The classification, enumeration, characteristics and economic performance of Alaska shellfish vessels. Part 1-Classification, enumeration and vessel characteristics. Norfish Tech. Rep. 61, 59 p.

[8]George M. Pigott, University of Washington, Department of Food Science, Seattle, WA 98195, pers. commun. December 1979.

[9]Sig Jaeger, President, North Pacific Vessel Owners Association, Fishermen's Terminal, Seattle, WA 98119, pers. commun. January 1980.

1) The maximum trip length when delivering at sea is limited only by the storage capacities for fuel, water, and supplies, while the maximum trip length when delivering onshore is limited by the iced storage life of the catch. In the first case, the maximum trip length has been estimated as 28 d for vessel type 1 and 26 d for vessel type 2. In the latter case, a 5-d storage life for fresh walleye pollock (Sea Fisheries Institute and National Marine Fisheries Service[10]) limits the trip to a maximum of 7 d (including time traveling to the grounds and time in port). At higher catch rates the actual trip length may be further limited by the hold capacity for groundfish and ice.

2) No ice is required when delivering at sea.

3) Fewer crew members are needed when delivering the catch at sea since no sorting or stowage of the catch is required. Jaeger[11] predicted that two fewer crew members would be required if delivering at sea. This proved true for at least one vessel owner participating in the joint venture for Pacific whiting (formerly known as Pacific hake) off the coast of Oregon during 1978 and 1979 (Fisher[12]). However, in this analysis, a conservative estimate of one fewer crew member has been adopted.

The search time, towing time, and the time in port have all been assumed to be the same for both modes of operation. The search time, or time spent prospecting for fish, and the time spent in port replenishing supplies, refueling, and unloading (if applicable) have been estimated to be 6 and 24 h, respectively. The towing time per day on the grounds has been taken to be 9 h after Jaeger (footnote 11). Again, these assumptions are conservative. If vessels delivering their catch at sea are fishing for a joint venture operation, the information sharing that is likely to occur may reduce the search time per trip. It has also been argued that the cod end transfer system employed in the sea delivery mode requires less rerigging time and therefore allows more towing time per day on the grounds (Fisher footnote 12).

[10]Sea Fisheries Institute, Gdynia, Poland, and National Marine Fisheries Service, Seattle, Wash. 1977. Preliminary report Gulf of Alaska research cruise. First leg, July 1977, 21 p.

[11]Jaeger, S. 1977. Presentation to the North Pacific Fishery Management Council on the subject of foreign joint ventures. August 5, 1977. Seattle, Wash.

[12]Barry Fisher, Vessel Owner/Operator, Newport, OR 97065, pers. commun. with R. Major, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, November 1979.

Fishing Strategy

Three different fishing strategies were examined based on the following stocks as targets: Pacific cod and walleye pollock in the western Gulf of Alaska, walleye pollock in the Aleutian area, and sole, especially yellowfin sole, *Limanda aspera*, in the eastern Bering Sea. The distances to the fishing grounds are based on the locations of the nearest of the most productive foreign fishing locations during 1977 and 1978 (Smith and Hadley[13]). Table 4 lists these locations and their approximate distances to the nearest port.

Fuel Price

For most of the following comparisons the fuel price was taken to be \$0.277/l, which was the current price for no. 2 diesel fuel at Dutch Harbor as of the time of this writing (1980). A subsequent section details the sensitivity of cost estimates to increases in fuel price.

RESULTS

Delivering at Sea Versus Delivering to Port

At any given catch rate for vessel type 1, the break-even ex-vessel price when delivering to a floating processor is at least 31% lower than when delivering to port. For example, at a catch rate of 10 t/d on the fishing grounds, vessel type 1 would require an ex-vessel price of \$421/t to cover costs if unloading in port while requiring only \$290/t if transferring the catch at sea. A plot of the relationship between break-even price and catch rate [described by Equation (1)] for vessel type 1 operating in the Gulf of Alaska delivering to a floating processor (solid) and delivering to a land-based processor (dashed) is shown in Figure 2.

Similar results were obtained from the analysis of vessel type 2 operating in the Gulf of Alaska (Figure 3). Under the sea delivery mode of operation break-even ex-vessel prices are at least 33% lower than under the port delivery mode. At a catch rate of 10 t/d the required break-even prices are \$146/t and \$217/t for sea delivery and port delivery, respectively. These results are in general agreement with Jaeger's (footnote 11) analysis in

[13]Smith, G. B., and R. S. Hadley. 1979. A summary of productive foreign fishing locations in the Alaska region during 1977-78: trawl fisheries. Alaska Sea Grant Rep. 79-7, 287 p.

TABLE 4.—Foreign catches from western Alaska waters during 1977 and 1978. Source: Smith and Hadley (text footnote 13).

Nation	Predominant species	Location		Nearest port	Distance (nmi)
		lat.	long.		
R.O.K.	Walleye pollock and Pacific cod	54°18′ N,	160°23′ W	Sand Point	75
U.S.S.R.	Walleye pollock and Pacific cod	56°30′ N,	152°30′ W	Kodiak City	75
Japan	Walleye pollock and Pacific cod	56°30′ N,	152°30′ W	Kodiak City	75
U.S.S.R.	Sole species	57°31′ N,	166°55′ W	Dutch Harbor	220
R.O.K.	Walleye pollock	53°25′ N,	166°15′ W	Dutch Harbor	65

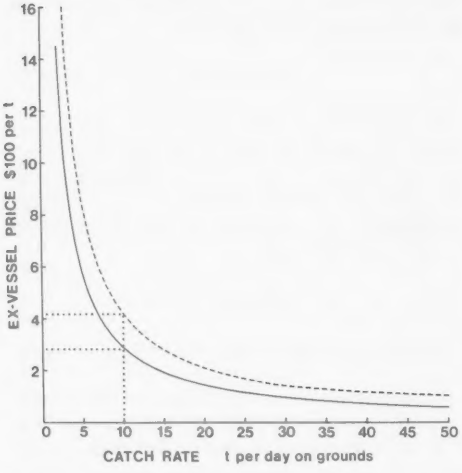

FIGURE 2.—Break-even price versus catch rate for vessel type 1, delivering to a floating processor (solid) and delivering to a shore-based processor 75 nmi from the fishing grounds (dashed). Dotted lines indicate required ex-vessel prices for a catch rate of 10 t/d.

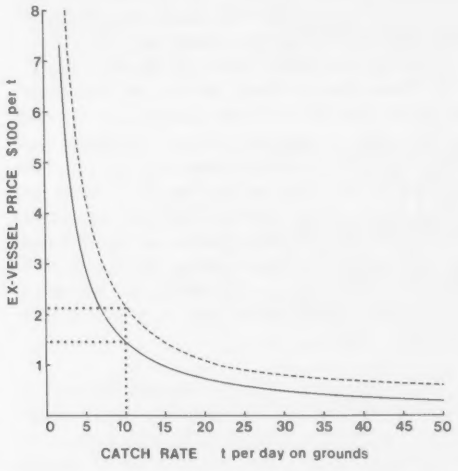

FIGURE 3.—Break-even price versus catch rate for vessel type 2, delivering to a floating processor (solid) and delivering to a shore-based processor 75 nmi from the fishing grounds (dashed). Dotted lines indicate required ex-vessel prices for a catch rate of 10 t/d.

which it was found that ex-vessel prices under the sea delivery mode could be 50% less than under the port delivery mode and still yield the same profit to the fisherman.

Another criterion for comparing harvest methods is the weight of whole fish harvested per volume of diesel fuel consumed, hereafter referred to as the fuel efficiency. At a catch rate of 10 t/d the fuel efficiency for vessel type 1 is 3.2 kg/l if delivering to port and 4.3 kg/l if delivering at sea. For vessel type 2 fuel efficiencies at 10 t/d are 4.0 kg/l and 5.5 kg/l for port and sea delivery modes, respectively. Thus, the fuel efficiencies increase by 34% (vessel 1) and 36% (vessel 2) under the sea delivery mode.

If the expected average catch rate is high (> 29 t/d for vessel 1 or >22 t/d for vessel 2), then the relative advantages of sea delivery increase since the hold capacity becomes limiting under the port delivery mode.

Comparison of Vessel Types

Based on the above results, it can be seen that the break-even price required by vessel type 2 is about 49% less than that required by vessel type 1, given the same catch rate. Alternatively, for any given ex-vessel price, the catch rate required by vessel type 1 to cover costs is about twice as high as that for vessel type 2. Furthermore, fuel efficiencies for the second vessel type are about 28% higher than those of vessel type 1.

Sensitivity to Changes in Fuel Price

The effect of changes in the price of fuel upon the relationship between the break-even price and catch rate will now be examined. For a given set of vessel characteristics and operating conditions, the fixed and variable costs are constant over a range of catch rates (assuming hold size is not limiting) and Equation (1) can be reduced to:

$$P = \frac{C_1}{U} + \frac{C_2 D}{U} \qquad (2)$$

where C_1 and C_2 are constants (C_2 = volume of fuel consumed), D = fuel price, P = break-even ex-vessel price, and U = total catch. Thus, the effect of the price of fuel upon the break-even ex-vessel price depends upon the catch rate and, of course, the vessel type and mode of operation. Once again using 10 t/d as a point of reference, Equation (2) predicts that for each \$0.026/l (\$0.10/gal) increase in the price of fuel, a \$6/t increase in the break-even ex-vessel price results (vessel type 1, delivering at sea, distance = 75 nmi). The same increase in fuel price for vessel type 1 unloading in port results in an \$8/t change in the break-even ex-vessel price. An equivalent increase in fuel price for vessel type 2 results in \$5/t and \$7/t increases in the break-even ex-vessel price for the sea delivery and land delivery modes, respectively. Thus, any estimates of economic feasibility will be moderately sensitive to changes in fuel price.

Comparison of Fishing Strategies

In the above comparisons, the distance from fishing grounds to the nearest port was fixed at 75 nmi, which is the expected distance if targeting on Pacific cod and walleye pollock in the western Gulf of Alaska. For the two alternative strategies, targeting on walleye pollock in the Aleutians area and targeting on yellowfin sole in the eastern Bering Sea, the expected distances are 65 and 220 nmi, respectively (Table 4). Accordingly, the model was run and Equation (1) was solved for a range of catch rates using these latter distances.

Figure 4 shows the ex-vessel prices required by vessel 1 under both modes of operation when the distance is 65 nmi and when the distance is 220

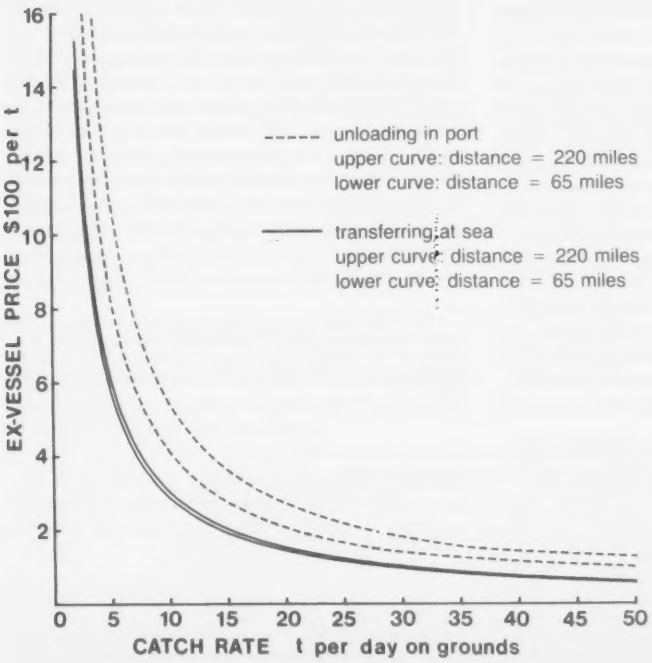

FIGURE 4.—Break-even price versus catch rate for vessel type 1, sea delivery and shore delivery, for distances of 65 and 220 nmi to the nearest port.

nmi. Similar curves result for vessel 2. It can be easily seen that under the port delivery mode a large increase in break-even price results from increasing the distance from 65 to 220 nmi (at 10 t/d these prices are \$414/t and \$545/t, a 32% increase). Under the sea delivery mode, however, the increased distance results in only a 6% increase in price (\$289/t to \$305/t at 10 t/d). Thus, any estimates of feasibility for the sea delivery mode are liable to be insensitive to changes in the distance to the fishing ground.

Feasibility of Groundfish Harvest

Table 5 lists the average species composition of the catches of three U.S. vessels fishing for two joint venture corporations in the Gulf of Alaska during 1979 and presumably targeting on Pacific cod and walleye pollock. In addition, the species composition obtained by Soviet factory trawlers targeting on sole in the Bering Sea and Korean factory trawlers targeting on walleye pollock in the Aleutians during 1978 is given (National Marine Fisheries Service[14]). Also listed in Table 5 are the ex-vessel prices offered by one of the joint venture firms as of the end of 1979. If U.S. trawlers catch the same species mix and receive the same prices, the expected average ex-vessel price per metric ton will be \$169 if targeting on Pacific cod and walleye pollock, \$217 if targeting on sole, and \$121 if targeting on walleye pollock. Table 6 presents the average catch rates, as predicted by the model, which would allow owners of vessel types 1 and 2 to break even, given the expected ex-vessel price and operating conditions for each of the three targeting strategies. I would now like to determine if these catch rates are feasible. Unfortunately, since the trawl fishery for groundfish in western Alaska is new to U.S. vessels, there is a paucity of U.S. commercial catch rate data.

Although the average catch rate for the three U.S. vessels fishing for joint ventures in 1979 was not available, a single U.S. vessel (25 m in length) fishing experimentally for one of the joint venture companies in the Shumagin area during 1978 averaged 11.8 t/d on the grounds. This vessel fished for only a short period, but the catch rate steadily increased from 4.8 to 22.3 t/d as the weather improved and experience was gained (Ely[15]). In light of these results, the catch rates of 17 and 9 t/d required by vessel types 1 and 2, if targeting on Pacific cod and walleye pollock and delivering to a floating processor, are considered feasible. Even the catch rates of 25 and 13 t/d required by the same vessels if landing their catch in port may be feasible; however, the vessel owner's margin for profit (if any) is substantially reduced. Again, these catch rates are fairly sensitive to the price of fuel (considered here to be \$0.277/l). An increase in the price of fuel to, say, \$0.528/l (\$2.00/gal) without a subsequent increase in groundfish prices, would lead to required catch rates of 21 and

[14]National Marine Fisheries Service, Foreign Observer Department. 1980. Unpubl. manuscr., n.p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[15]R. C. Ely, American Fisheries Corporation, Anchorage, AK 99503. Report on progress of the KMIDC/Davenny pollock joint venture in the Gulf of Alaska. Report given to the North Pacific Fishery Management Council in public hearings. November 30, 1978.

TABLE 5.—Recent ex-vessel prices offered by a joint venture corporation and average species composition and average catch rates of groundfish taken by: 1) U.S. vessels fishing for joint ventures in the Gulf of Alaska during 1979, 2) Soviet factory trawlers fishing in the eastern Bering Sea during 1978, and 3) Korean factory trawlers fishing in the Aleutians area during 1978. Source: National Marine Fisheries Service (text footnote 14).

Species	Ex-vessel price	Percentage composition		
		U.S.	U.S.S.R.	R.O.K.
Walleye pollock	\$132	38.5	4.1	84.2
Pacific cod	187	47.0	2.1	5.1
Sole[1]	242	5.0	85.9	0
Rockfish	308	6.0	0	.1
Others	—	3.5	7.9	10.6
Catch rate, t/d		11.8	43.2	61.0

[1]Yellowfin sole and Alaska plaice.

TABLE 6.—Expected ex-vessel prices and required break-even catch rates by target strategy, vessel type, and mode of operation.

Target species	Area	Price/t	Vessel type	Required break-even catch rate (t/d on grounds)	
				Sea delivery	Land delivery
Pacific cod and walleye pollock	Gulf of Alaska	169	1	17	25
			2	9	13
Sole species	Bering Sea	217	1	14	25
			2	7	14
Walleye pollock	Aleutian Islands	121	1	24	37
			2	12	17

12 t/d for the two vessel types if delivering at sea and 30 and 17 t/d if delivering to port.

The catch rates that can be expected by U.S. groundfish trawlers operating in the Bering Sea and Aleutians are even more nebulous. The Soviet trawlers targeting on sole in the Bering Sea during 1978 were much larger (76-89 m, 2,000 hp) than the U.S. trawlers under consideration (Pruter[16]). However, much of the factory trawler's size is devoted to supporting crews of 87-96 for periods up to 90 d at sea. In addition, these vessels must have space for large processing and storage facilities. The U.S. vessels, on the other hand, with crews of four or five and no processing facilities, are more efficient for their size as catchers. Therefore, the break-even catch rates of 14 and 7 t/d for vessel types 1 and 2 targeting on sole and delivering to sea seem quite feasible when compared with the Soviet's average of over 43 t/d. Even though the catch rates required if delivering to port (25 t/d for vessel type 1, 14 t/d for vessel type 2) are nearly twice as high as required when delivering at sea, they still may be considered feasible when compared with the average Soviet catch rate.

If instead, U.S. trawlers similar to types 1 and 2 target primarily on walleye pollock in the Aleutians as did large Korean factory trawlers (89-111 m, 3,500-6,000 hp, Pruter footnote 16) the U.S. vessels would require catch rates of approximately 24 and 12 t/d if delivering at sea. The corresponding catch rates if delivering to port are 37 and 17 t/d. Although these catch rates are higher than under the previous strategies, they may be feasible considering the high availability of walleye pollock in the area. In fact, none of the above catch rates can be considered unfeasible since the average Korean catch rate in the Aleutian area exceeded 61 t/d.

DISCUSSION

Recently a number of events have occurred which have made fishing for groundfish in western Alaska relatively more attractive.

1) A market for potentially large quantities of groundfish has developed with the initiation of the two international joint ventures in western Alaska.

2) Groundfish markets in California, Oregon, and Washington have been erratic and prices have been generally low (Sorensen[17]).

3) Vessel profits from the western Alaska shellfisheries have decreased due to:

a) declining abundance of pandalid shrimp (Jackson et al.[18]) and snow crab stocks (Somerton[19]),

b) a drop in the ex-vessel price for king crab from $2,460/t ($1.23/lb) in 1978 to $1,720/t ($0.86/lb) in 1979 (Browning[20]), and

c) expansion of the king crab fleet (from 60 boats in 1977 to 226 in 1979) leading to shortened seasons and reduced average vessel shares of the relatively constant quota.

The results of this analysis indicate that given a market with ex-vessel prices similar to those being offered by the joint venture firms, U.S. fishermen may currently find it economically attractive to participate in a trawl fishery for groundfish in western Alaska. In fact, some 23 vessels are committed to fish for the joint venture operations in western Alaska during 1980 (Blackburn[21]). It would seem, from this analysis, that operators of vessels similar to vessel types 1 or 2 can currently cover both fixed and variable costs given the above ex-vessel prices whether delivering at sea or delivering to port. However, the profits if delivering to port would be less. To equal the vessel profits under the sea delivery mode, land-based processors would have to offer ex-vessel prices at least 45% higher than those offered at floating processors would have to offer ex-vessel prices at least delivering at sea should increase with increased fuel costs. As fuel prices increase, owners of larger vessels with high horsepower, such as vessel type 1, will have a harder time making a profit in a western Alaska groundfish trawl fishery than owners of smaller vessels such as type 2.

This paper has not examined the economic feasibility of domestic processors. However, since

[16]Pruter, A. T. 1980. Preliminary analysis of data obtained by foreign fishery observers in 1978. Processed Rep. 80-7, 58 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

[17]Sorensen, S. 1979. Statement to the International Trade Commission. Reprinted in Alaska Fisherman's J. 2(12):20-21.

[18]Jackson, P. B., P. Holmes, A. Spalinger, and J. Nickels. 1979. Shrimp research. *In* Westward Region Shellfish Report to the Alaska Board of Fisheries, April, 1979, p. 216-242. Alaska Dep. Fish Game, Kodiak.

[19]Somerton, D. 1979. A reappraisal of the declining trend of recruitment to the Bering Sea stock of tanner crab (*Chionoecetes bairdi*). Norfish Tech. Rep. 92, 16 p.

[20]Browning, R. 1979. Crab season cut short as Bering boats fill quota. Natl. Fisherman 60(8):11.

[21]Blackburn, C. 1979. Plans progress for KMIDC fish purchases. Kodiak Daily Mirror 39(185):1-3.

U.S. fishermen are restricted by law to using only U.S. built vessels for fishing related activities, any domestic floating processors are likely to be either new vessels or extensive conversions, both of which may be cost prohibitive. On the other hand, distant water fishing nations, faced with increasing area and quota restrictions, may have factory vessels which are receiving less than optimal use (Kaczynski and LeVieil[22]). For this reason, international joint fishing ventures may be the only viable option for potential domestic groundfish trawlers in western Alaska in the near future. Although it has been argued that international joint fishing ventures may hinder the development of domestic land-based processors (Sullivan and Heggelund 1979), and the long-term net benefits to the domestic industry as a whole may be negative (Gorham footnote 2), the immediate benefits to the U.S. fishermen involved are positive.

CONCLUSIONS

On the basis of the economic model and assumptions applied in this study it was shown that:

1) Delivering the catch at sea via detachable cod ends is more economically efficient for U.S. fishermen than landing the catch in port. This is particularly true of fisheries for species with high spoilage rates, such as walleye pollock. The cost savings in this analysis amounted to over 30% and derive primarily from the following factors:

   a) Fewer crew members are required when delivering the catch at sea.
   b) A much higher percentage of the season can be devoted to trawling time when delivering to a sea-based processor.
   c) Less fuel per season is spent running back to port, thus the fuel efficiency is greater when delivering the catch at sea.

These cost savings apply whether fishing for an international joint fishing venture or delivering the catch to a domestic floating processor.

2) Increasing the distance to the fishing grounds, while largely affecting the economic efficiency if delivering to port, had little effect if delivering at sea.

3) The relationship between catch rate and break-even ex-vessel price is sensitive to increases in fuel price for both the sea delivery and land delivery mode of operation. However, it is slightly less critical for the sea delivery mode. Each increase of $0.026/l ($0.10/gal) should lead to an increase of $6/t in the break-even ex-vessel price for a vessel similar to type 1 delivering at sea (distance to grounds = 75 nmi) and averaging 10 t/d. For the same vessel delivering to port, such an increase in fuel price should lead to an increase in $8/t in the required ex-vessel price.

4) Fuel efficiencies (weight of fish caught per volume of fuel consumed) were 28% higher for vessel type 2 (25-28 m) than for vessel type 1 (33 m), and were about 35% higher for both vessels for sea delivery than for port delivery.

5) U.S. fishermen operating vessel types similar to the 33 m crabber/trawler and the 25 m trawler considered in this analysis may find it economically attractive to participate in joint fishing ventures for groundfish in the western Gulf of Alaska and the eastern Bering Sea given the ex-vessel prices currently being offered by the joint venture companies and the large volumes of fish in which these companies are interested.

It was considered feasible for these U.S. vessels to attain average catch rates sufficiently high to cover the fixed and variable costs of fishing under each of three fishing targeting strategies in which the target stocks are: 1) Pacific cod and walleye pollock in the western Gulf of Alaska, 2) sole in the eastern Bering Sea, and 3) walleye pollock in the Aleutians area.

ACKNOWLEDGMENTS

I would like to thank S. Jaeger, V. Kaczynski, and G. M. Pigott for contributing helpful information and suggestions during the development of this paper. Thanks are also due to D. Somerton and L. J. Bledsoe for their helpful critiques.

The research for this paper was supported by the University of Washington Sea Grant Program (Grant No. NA-79-AA-00054) through subgrants extended to the Institute for Marine Studies (Grant No. R/MS-6) and the Norfish Research Group (Grant No. R/F-9).

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APPENDIX I.—COST DERIVATIONS AND SOURCES OF ESTIMATES

I. A. Boat and engine routine maintenance. 7% of the vessel's initial value (VIV) is based on Marine Economics Data Sheets[23-27] for bottom draggers which indicate boat and engine repairs ranging from 5.1 to 11.4% (average 7.0%) of the vessel's market value. Katz and Lee[28] used a "rough estimate" of 6% for crab vessels.

B. Insurance. 2.1% of VIV for hull is a midpoint estimate based on a range of 1.7 to 2.5% (Jaeger footnote 11; Katz and Lee footnote 28).

C. Depreciation. Based on the following assumptions for vessel type 1 (Jaeger footnote 9):

	Cost	*Useful life (yr)*
Electronics	$ 100,000	6
Engine	$ 250,000	10
Hull	$1,150,000	30

Over a 30-yr period, assuming constant replacement costs, costs due to depreciation will be 5 × $100,000 + 3 × $250,000 + $1,150,000 = $2,400,000. The yearly cost is then $80,000 which equals 0.0533 VIV. Assuming equal cost proportions for vessel type 2 (electricity 6.7%, engine 16.7%, and hull 76.6% of VIV) also yields 0.0533 VIV.

D. Association dues. From Katz and Lee (footnote 28) updated to current values based on insurance cost index (U.S. Bureau of the Census 1978).

E. Contingencies/Miscellaneous. From Smith.[29]

F. Average annual cost of financing. Assumes 80% VIV financed and amortization through equal monthly payments. Financing for vessel type 1 is for 20 yr at 10% annual interest. Financing for vessel type 2 is for 15 yr at 8.5% interest. Differences in interest rates are due to different times of purchase.

[23]Marine Economics Data Sheets. 1971a. Seattle drag fishing business. Oregon State University Extension Service SR500-9.
[24]Marine Economics Data Sheets. 1971b. Seattle drag fishing business. Oregon State University Extension Service SR500-10.
[25]Marine Economics Data Sheets. 1971c. Seattle drag fishing business. Oregon State University Extension Service SR500-11.
[26]Marine Economics Data Sheets. 1971d. Seattle drag fishing business. Oregon State University Extension Service SR500-12.
[27]Marine Economics Data Sheets. 1977. Charleston drag fishing business. Oregon State University Extension Service SR500-19.
[28]Katz, P. L., and C. L. Lee. 1976. Computing annual return to vessel investment in a fisheries economic projection model—demonstration of method, based on a vessel in the Bering Sea king crab fishery. Norfish Tech. Rep. 63, 10 p.
[29]Smith, F. J. 1978. Understanding and using marine economics data sheets. Oreg. State Univ. Sea Grant Spec. Rep. 500, 4 p.

II. A. Gear repair and replacement. It is generally agreed that fishing gear maintenance and repair is roughly proportional to the amount of fishing time, but very little data are available which describe this relationship. The estimate of $20.57/h for vessel type 1 is based on the following estimates of Jaeger (footnote 11):

Total gear maintenance costs per year	$20,000
Total towing hours per year	972

The hourly costs for vessel type 1 are taken to be the same ($20,000/972) as for the vessel described by Jaeger. Since the trawl used by vessel type 2 would be smaller and hence less expensive than that of vessel type 1, its hourly costs were reduced by a factor based on the values of one net (including roller gear and floats) as estimated by Hurd.[30]

	Value of net
Vessel type 1	$7,000
Vessel type 2	$5,500-$6,000

B. Fuel costs. Gal/h:hp ratios as estimated by Jaeger (footnote 9). Fuel price of $0.277/l ($1.05/gal) based on current price at Dutch Harbor, Alaska.

C. Food costs. Based on Katz and Lee (footnote 28) and Jaeger (footnote 11) and updated by cost index (U.S. Bureau of the Census 1978).

D. Ice. Based on Bledsoe and Mesmer[31] and updated by cost index (U.S. Bureau of the Census 1978).

E. Crew and captain's shares. Katz and Lee (footnote 28), Jaeger (footnote 11).

[30]Rod Hurd, Seattle Marine and Fishing Supply Co., Seattle, Wash., pers. commun. December 1979.

[31]Bledsoe, L. J., and K. Mesmer. 1978. Summary of regional fishery system simulator configuration for N.E. Pacific shellfishery studies (NEPAC model and simulator). Norfish Pap. NM46, 19 p.

A STOCHASTIC MODEL FOR THE SIZE OF FISH SCHOOLS[1]

JAMES JAY ANDERSON[2]

ABSTRACT

A model is presented that reproduces the frequency distribution of fish school diameters observed acoustically in waters off southern California. The rate of change of school diameter is described by an equation that includes an entrance rate of fish into a school, which is independent of the number of fish in the school, and an exit rate, which is proportional to the number. The number in a school is assumed to be proportional to the square of the school diameter implying the average shape is disklike. Fluctuations in school size from unknown factors are approximated by stochastic rate terms for the entrance and exit rates and the diameter-number relation. This gives a stochastic dynamic equation for the rate of change of diameter and the probability distribution of the diameter is analyzed with a Fokker-Planck probability equation. A sensitivity analysis indicates two basic distribution types occur. Large exit rates and small stochastic fluctuations produce a narrow range of small diameters, while large entrance rates and large fluctuations produce a wide range of large diameters. Qualitative inferences from the model indicate schools of large fish should have a wide range of large diameters while small fish should have a narrow range of small diameters. Also fishing activity could decrease entrance rates and increase exit rates, and the combination would shift the probability distribution to a narrow range of small diameters.

When fish are mutually attracted they form schools, either in random orientation or in highly organized structures (Shaw 1978). The shape of the schools are diverse and changeable, and typically range from ribbonlike to spherical with the latter being uncommon (Radakov 1973). The attraction is mostly keyed visually and in northern anchovy, *Engraulis mordax*, schools off southern California the shape is disklike during the day and generally more diffuse and elongated at night (Squire 1978). Often within a school fish arrange in a lattice structure with the density of fish per unit volume related to fish length (Breder 1976; Serebrov 1976).

Models for the interactions of fish in a school have been postulated by a number of authors (see Breder 1976 for review and Okubo et al. 1977), but the processes controlling the size of a school in terms of the number of fish in a school or its physical dimensions have not been considered in mathematical terms. Considering what factors may be important in controlling size it is apparent the problem is complex and could include species behavior, light, predator-prey interactions, turbulence, life cycle stages, the stock population, and the size of the schools themselves.

An interesting set of observations on the size-frequency distribution of unidentified schools off southern California, shows a well-defined peak frequency at a diameter of about 15 m (Smith 1970). Towards larger and smaller diameters the frequency distribution decreases in an exponentiallike manner (Figures 1, 2).

This simple, and relatively stable, distribution is particularly interesting considering the possible complexity of the schooling process. The observations might be produced in one of two funda-

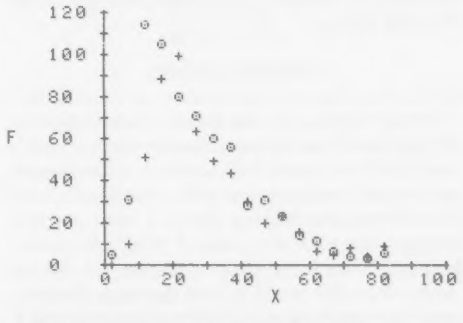

FIGURE 1.—Frequency distribution of fish schools (F) vs. school diameter (X) for unidentified schools observed with sonar by Smith (1970) from San Francisco, Calif., to Cabo San Lazaro, Baja California, in May 1969 (⊖) and June 1969 (+). F in numbers of schools and X in meters.

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[2]Fisheries Research Institute, University of Washington, Seattle, WA 98195.

Manuscript accepted September 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

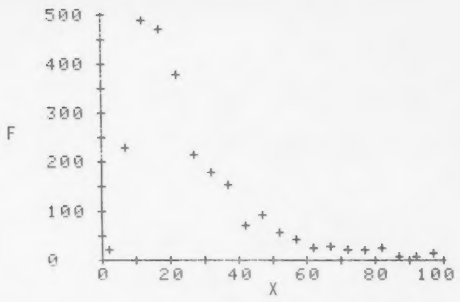

FIGURE 2.—Frequency distribution of fish schools (F) vs. school diameter (X) for composite of Smith's (1970) sonar surveys off California and Mexico in January, February, April, May, June, and July 1969.

mental ways. Either the frequency distribution is coupled to the school size or it is coupled to other factors such as the species composition of the observations. In the first case, the factors relating to environmental conditions, species, and stock numbers may also be acting on the school size but could be hidden in the averaging, inherent in the frequency mode of data display. In the second case, size may be insignificant and the distribution might reflect other factors. For example, if each species has a preferred school size, then a particular frequency distribution of species could produce an apparent frequency size correlation.

In this paper I explore the situation where the schooling dynamics are dependent on the school size and other factors, like species composition, have effects randomly distributed over the range of school sizes.

OBSERVATIONS

Smith (1970) observed fish schools over a 200,000 nmi^2 area between San Francisco, Calif., and Cabo San Lazaro, Baja California. The targets were recorded using sonar with a transducer fixed at a 90° relative bearing giving a beam perpendicular to the path of the ship. A 30 kHz frequency was used with a 10° conic beam (at −3 dB), at ranges from 200 to 450 m from the ship. Observations were made during daylight hours only and a complete survey of the area could be made in <2 mo. The dimensions of the schools were measured at right angles and parallel to the ship and the number of schools in 5 m intervals of diameter was estimated, correcting for bias from schools that only fell partially within the 200-450 m observation window of the sonar.

Frequency distributions for surveys in May and June 1969 were composed of 525 and 650 observations, respectively, in the diameter range 0-99 m (Figure 1). A composite frequency distribution of surveys in January, February, April, May, June, and July 1969 contained 2,549 observations of schools between 0 and 99 m diameter (Figure 2).

Smith (1970) estimated to a first order that about 30% of the observed schools were adult northern anchovy. Other common schooling fish in the area, the CalCOFI area, include northern anchovy juveniles; jack mackerel, *Trachurus symmetricus*, juveniles; Pacific bonito, *Sarda chiliensis*; Pacific mackerel, *Scomber japonicus*; and Pacific sardine, *Sardinops sagax*.

THE MODEL

To describe the frequency distribution of school diameters first consider an equation for the rate of change of the number of fish in a school. Define this rate in terms of a deterministic equation, which is related to school size, plus a stochastic equation which is taken to approximate the remaining unknown fluctuating behavior of the rate. The deterministic and stochastic equations are combined to give a stochastic dynamic equation for the rate of change of fish in a school as

$$\frac{dN}{dt} = \alpha + \delta(t) - \beta N + \gamma(t)N. \qquad (1)$$

The number of fish in a school is N and its change with time is determined as the difference between the rate fish enter the school, which is independent of N, and the rate fish exit from the school, which is proportional to N. The deterministic entrance and exit rates are α and βN where α and β are constant and represent averages over an ensemble of schools. The stochastic entrance and exit rates are $\delta(t)$ and $\gamma(t)N$ where $\delta(t)$ and $\gamma(t)$ represent white noise fluctuations which vary rapidly compared with variations in N, and are not affected by past conditions. The mean values of the stochastic terms are zero and so the stochastic parts represent fluctuations about the deterministic rate terms.

To express the frequency distribution in terms of school diameters we note Squire's (1978) observations in which the average shape of northern an-

chovy schools during the daylight hours is disklike. Including unknown factors that alter the three-dimensional shape through a stochastic term the relation between the school diameter and number is expressed as

$$N = X^2(\rho + \epsilon(t))\ \pi/4 \tag{2}$$

where X is the diameter of a school with a disklike shape, ρ is the average density of fish per unit horizontal area, and $\epsilon(t)$ is the stochastic variation on the density and has white noise character. Rewrite Equation (2) as

$$N = pX^2(1 + h(t)) \tag{3}$$

where p is a generalized density with $p = \rho\pi/4$ and $h(t)$ is the stochastic density normalized to p giving $h(t) = \epsilon(t)/p$.

Using Equation (3) in Equation (1) and differentiating yields

$$\frac{dX}{dt} = \frac{\alpha}{2pX(1+h(t))} - \frac{\beta X}{2} + \frac{\delta(t)}{2pX(1+h(t))} + \frac{\gamma(t)X}{2} + \frac{dh(t)/dt}{2(1+h(t))}. \tag{4}$$

To separate the deterministic and stochastic parts of Equation (4) assume $\rho > |\epsilon(t)|$ so $h(t)^2 < 1$ giving the convergent series

$$\frac{1}{1+h(t)} = 1 - h(t) + h(t)^2 - h(t)^3 + \ldots = 1 + \sum_{m=1}^{\infty} (-h(t))^m. \tag{5}$$

Using Equation (5) in Equation (4) and separating deterministic and stochastic parts in powers of X yields the stochastic dynamic equation for X as

$$\frac{dX}{dt} = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{i(t)}{2pX} + \frac{j(t)X}{2}. \tag{6}$$

The first term on the right side of Equation (6) is the deterministic expansion rate of a school and the second term is the deterministic contraction rate. The third term is the stochastic expansion rate and is principally related to the stochastic entrance rate. The stochastic component in expanded form is

$$i(t) = \delta(t) + (\alpha + \delta(t)) \sum_{m=1}^{\infty} (-h(t))^m.$$

The last term in Equation (6) is the stochastic contraction rate and is related to the stochastic exit rate according to the relation

$$j(t) = \gamma(t) + \frac{dh(t)}{dt} \sum_{m=0}^{\infty} (-h(t))^m.$$

We assume the components $i(t)$ and $j(t)$ are stationary random processes with zero mean values. Then their statistics can be characterized by the relations

$$\overline{i(t)i(t+t')} = \sigma_i^2\, q_i(t')$$

$$\overline{j(t)j(t+t')} = \sigma_j^2\, q_j(t') \tag{7}$$

where $\sigma^2{}_i$ and $\sigma^2{}_j$ are positive constants that quantify the level of the stochastic inputs and are referred to as "incremental variances." The $q(t')$ terms are autocorrelation functions that quantify the spectrum characteristics of the stochastic inputs as a function of separation time t'.

To investigate the probability characteristics of X in Equation (6) we must combine the stochastic terms into a single stochastic input, in a manner that retains the statistical characteristics of the terms. From Equation (7) we define the ratio

$$r(t')^2 = \frac{\overline{i(t)i(t+t')}}{\overline{j(t)j(t+t')}} = \frac{\sigma_i^2\, q_i(t')}{\sigma_j^2\, q_j(t')}.$$

We assume the correlation functions are similar enough to make the simplification $q_i(t')/q_j(t') \approx 1$. Then we relate the two stochastic terms in Equation (6) as

$$i(t) = rj(t) \tag{8}$$

where r is the ratio of the intensities of the inputs and is defined as

$$r = \sigma_i/\sigma_j. \tag{9}$$

In effect with Equations (8) and (9) we are taking the ratio of the two stochastic terms to be equal to

the ratio of their "incremental standard deviations." These are not the typical standard deviations, but if the correlation functions q_i and q_j are similar the ratio of the incremental standard deviations should approach the ratio of the typical standard deviations of the variables, i.e., $r \rightarrow \mathrm{SD}(i(t))/\mathrm{SD}(j(t))$ as $q_i(t')/q_j(t') \rightarrow 1$.

Now the stochastic dynamical equation for fish school diameter is written

$$\frac{dX}{dt} = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{j(t)}{2}\left[\frac{r}{pX} + X\right]. \quad (10)$$

The probability characteristics of X can be analyzed according to the Fokker-Planck equation (Goel and Richter-Dyn 1974). This is also known as the forward diffusion equation for probability in X and t. The probability density for the system having a diameter X at time t when it had diameter Y at time zero is denoted $P(X/Y,t)$ and for Equation (10) the Fokker-Planck equation is

$$\frac{\partial P(X,t)}{\partial t} = -\frac{1}{2}\left\{\frac{\partial}{\partial X}\left[\left[\frac{\alpha}{pX} - \beta X + \frac{\sigma^2}{8}\frac{\partial}{\partial X}\left(\frac{r}{pX} + X\right)^2\right]P(X,t)\right]\right\} + \frac{\sigma^2}{8}\frac{\partial^2}{\partial X^2}\left(P(X,t)\left(\frac{r}{pX} + X\right)^2\right). \quad (11)$$

The term σ^2 is the incremental variance of the diameter shrinkage rate and is in fact equivalent to σ^2_j in Equation (7). The term has a dimension of t^{-1} and is also the diffusion coefficient of probability $P(X,t)$ in X space. In this manner it quantifies the level of randomness in the schooling process.

For the Fokker-Planck equation the growth rate of the mean value of X is

$$M_1(X) = \frac{\alpha}{2pX} - \frac{\beta X}{2} + \frac{\sigma^2}{2}(r/pX + X)(1 - r/pX^2) \quad (12)$$

and the growth rate of the variance of X is

$$M_2(X) = \frac{\sigma^2}{4}(r/pX + X)^2. \quad (13)$$

From the similarity of frequency distributions for different months (Figures 1, 2) we assume a steady-state probability distribution and from Goel and Richter-Dyn (1974) this is expressed as

$$P(X) = \frac{C}{M_2(X)} \exp\left\{\int_0^X 2\frac{M_1(s)}{M_2(s)}\, ds\right\} \quad (14)$$

where C is a constant determined by the condition that the total probability equals one

$$1 = \int_0^\infty P(X)dX. \quad (15)$$

Using Equations (12) and (13) in Equation (14) the steady-state probability distribution, or probability density, for school diameter is

$$P(X) = \frac{kXe^{-2(a+bc)/(c+X^2)}}{(c+X^2)^{(1+2b)}} \quad (16)$$

where

$$a = \alpha/p\sigma^2,\ b = \beta/\sigma^2,\ c = r/p,$$
$$k = 4C/\sigma^2. \quad (17)$$

The dimensions of the above constants with l for length, t for time, and n for number of fish are as follows. The parameters a and c have dimensions of l^2, b is dimensionless, and k has dimensions of l^{1+4b}. The dimension of α is lt^{-1}, β and σ^2 have t^{-1}, p has nl^{-2}, r has n, and C has $t^{-2}l^{1+4b}$.

FITTING THE MODEL TO DATA

Equation (16) can be fit to Smith's (1970) data through a number of methods all of which adjust the free parameters a, b, and c to obtain a best fit according to visual or statistical criterion. To obtain a first order estimate of the free parameters we will use a simple algorithm in which the probability curve is made to go through the observed

probability distribution at the most common, or peak, diameter and one other diameter in the distribution. This fixes two of the free parameters and with trial values of the remaining free parameter the model is fit to observations.

We begin by converting the probability equation to the frequency equation

$$F(X) = \frac{k^*}{k} P(K) \tag{18}$$

where $F(X)$ is the number of fish observed at diameter X and k^* is a constant that is a function of the number of schools observed. At the most common diameter X_0, the frequency is maximum so $dF(X_0)/dX = 0$ and from Equations (16) and (18) we obtain

$$a = X_0^2 \left(b + \frac{1}{4}\right) - \frac{1}{4} c^2/X_0^2. \tag{19}$$

With Equation (19) in $F(X)$ the log of $F(X)$ yields equations for b and k^*. These can be solved explicitly with observations $F(X_0)$, $F(X_1)$, X_0, X_1, and the free parameter c where X_1 is a diameter greater than the peak diameter X_0. The equations are

$$b = \frac{A(X_1) - A(X_0) + C(X_1) - C(X_0)}{B(X_1) - B(X_0)} \tag{20}$$

$$k^* = \exp\left\{-A(X_0) + bB(X_0) - C(X_0)\right\} \tag{21}$$

where $A(X_i) = \frac{1}{2}(c^2/X_0^2 - X_0^2)/(c + X_i^2) + \ln(X_i/(c + X_i^2)$

$B(X_i) = 2(c + X_0^2)/(c + X_i^2) + 2\ln(c + X_i^2)$

$C(X_i) = -\ln(F(X_i))$

with $i = 0$ and 1.

For the composite of observations depicted in Figure 2 we take $X_0 = 14$ m, $X_1 = 40$ m, $F(X_0) = 491$, and $F(X_1) = 115$. A good fit (Figure 3) is obtained with $c = 60$ m^2 and the remaining constants from Equations (19), (20), and (21) are $a = 133$ m^2, $b = 0.452$, and $k^* = 4716244$.

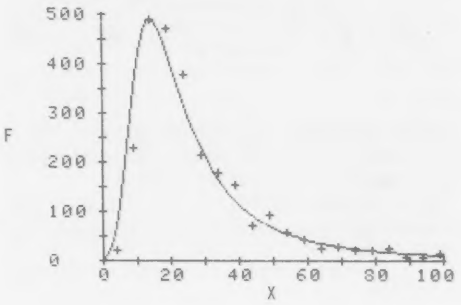

FIGURE 3.—Fit of probability equation of school diameter to frequency distribution of Figure 2. Probability Equation (16) is equated to frequency according to Equation (18).

SENSITIVITY ANALYSIS

The sensitivity of $P(X)$ to variations in the model parameters has been investigated for $P(X)$ in the configuration of the observed distribution (Figure 3).

We note that the curve $P(X)$ is defined by three free parameters a, b, and c which are in effect fitting parameters. These are ratios of the coefficients of the stochastic dynamic Equation (10). The coefficients are the dynamic parameters of the system and are α, β, σ, σ_i, and p. The relationship between the fitting parameters and the dynamic parameters is given by Equation (17) where σ_i is related to r by Equation (9). Because the dynamic parameters are only known in ratios in this model we can only investigate their effect on $P(X)$ in terms of relative changes. The relative value y', of a dynamic parameter y, can be defined

$$y' = y/y_o \tag{22}$$

where y_o is the value of the dynamic parameter corresponding to the fit to the observed frequency distribution.

To investigate the equation sensitivity, each dynamic parameter is varied while the others are held constant at their y_o values. For each set of

dynamic parameters generated in this manner $P(X)$ is calculated for X from 0 to 100 m. For each set of parameters the constant k in Equation (16) is determined according to the condition expressed by Equation (15) by numerically integrating the integral

$$1/k = \int_0^{X^*} \frac{Xe^{-2(a+bc)/(c+X^2)}}{(c+X^2)^{(1+2b)}}\, dX\,. \qquad (23)$$

Using Simpson's rule for integration $1/k$ is evaluated within a few percent accuracy with a 1 m integration step and $X^* = 300$ m.

The response of $P(X)$ to variations in the dynamic parameters is illustrated in Figures 4-8,

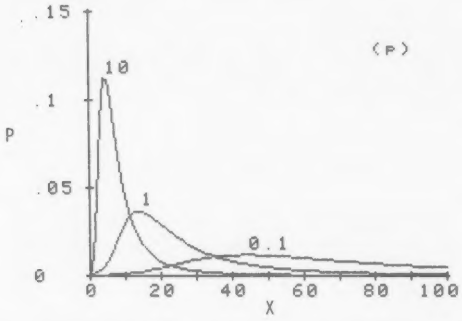

FIGURE 4.—Probability distribution (P) vs. school diameter (X), in meters, for relative schooling density parameter values p′ = 0.1, 1, and 10.

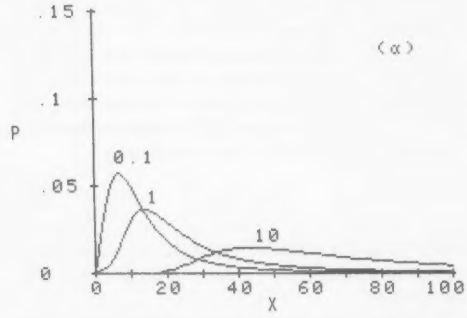

FIGURE 5.—Probability distribution (P) vs. school diameter (X) for relative entrance rate values $\alpha' = 0.1$, 1, and 10.

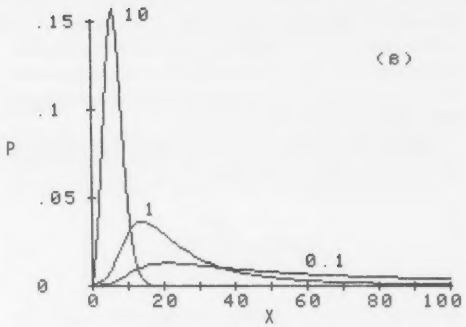

FIGURE 6.—Probability distribution (P) vs. school diameter (X) for relative exit rate parameter values $\beta' = 0.1$, 1, and 10.

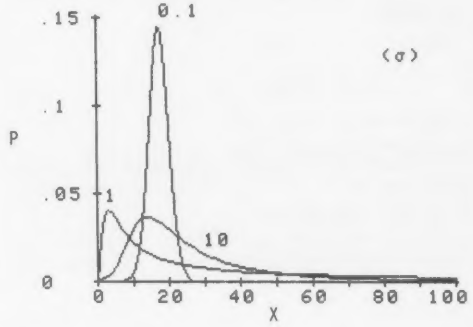

FIGURE 7.—Probability distribution (P) vs. school diameter (X) for relative shrinkage rate standard deviation values $\sigma' = 0.1$, 1, and 10.

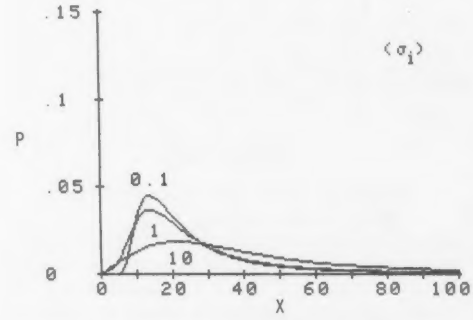

FIGURE 8.—Probability distribution (P) vs. school diameter (X) for relative expansion rate standard deviations values $\sigma'_i = 0.1$, 1, and 10.

which show $P(X)$ vs. X for each parameter varied with relative values $y' = 0.1, 1, 10$, where $y' = 1$ is the relative value corresponding with the fit to the observed distribution (Figure 3). In the figures the shape of $P(X)$ varies between a well-defined sharp peak, in which only a narrow range of diameters are probable, and a broad low peak, in which a larger range of somewhat larger diameters are probable. A brief discussion of the sensitivity and some possible biological implications follows.

p

The density, or number of fish per square meter of horizontal area of a school, has a strong effect on the probability distribution (Figure 4). A dense grouping of fish, corresponding with large values of p, favors a narrow range of small school diameters while a low density favors a wide range of larger diameters. Serebrov (1976) illustrated that the density of fish in a school is highly correlated to fish length according to the relation $\rho = 1/(LK)^3$ where ρ is the density in number of fish per cubic meter, L is fish length in centimeters, and K is a constant, with average value 2.44. If we assume the density per square meter is proportional to the density per cubic meter, then with Serebrov's relation, p responds to the one-third power of fish length averaged over the ensemble of schools making up the observations. Fish length becomes a sensitive parameter, e.g., the relative change in p from 1 to 10 in Figure 4 corresponds to a relative change in the average fish length from 1 to 0.46.

α

For small values of the entrance rate into schools, small diameters are favored, and as the entrance rate increases a wide range of large schools is favored (Figure 5).

The rate α has units of number of fish entering the school per unit time, and if we envision the entrance event as the chance encounter and joining of two schools, then α should be proportional to the average number of fish in the schools divided by the average time interval between encounters of schools. The time interval between encounters could decrease as the stock population increases if the number of schools per unit area increases. Thus, the entrance rate could increase with increases in the stock population of an area. This reasoning suggests that larger stocks would contain a wide range of school sizes and small stocks would contain a narrow range of small school sizes.

β

The parameter β is the coefficient for the average exit rate of fish from a school and has units of t^{-1}. If we envision the loss mechanism as a random dividing of the school into two fractions, with the time interval between the divisions being random, then the average time interval is proportional to β^{-1}. Thus, larger values of β correspond to short time intervals between divisions and small values correspond to large time intervals between school divisions. The interval as expressed by β has a significant effect on the probability distribution $P(X)$, with small values favoring a narrow range of small diameters and large values favoring a wide range of larger diameters (Figure 6).

σ

The randomness in the schooling process is quantified in the model by the incremental standard deviation σ, which has units of $t^{-1/2}$. For small levels of randomness, small σ, the probability distribution converges on the deterministic steady-state diameter which is defined

$$\bar{X}_0 = (\alpha/p\beta)^{1/2} = (a/b)^{1/2}.$$

For the model fit this gives $\bar{X}_0 = 17.3$ m. The convergence is evident in Figure 7 in which X_0 changes from 3 to 14 to 17 with σ changing from 10 to 1 to 0.1. At larger values of σ the system has more random character and the probability distribution spreads away from the deterministic value $\bar{X}_0$. Expressed as the incremental variance σ^2, with the dimension t^{-1}, the term is the diffusion coefficient of probability in X space, since the Fokker-Planck equation is in fact a diffusion equation of probability in X and t.

σ_i

The incremental standard deviation of the expansion rate, σ_i is defined by Equation (7) and is related to the probability equation through r according to Equation (9). It has a small effect on the probability distribution with larger values producing a broadening of the probability distribution and a shift towards larger diameters. Increasingly, smaller values asymptotically approach a stable

distribution as is evident by the similarity of the curves for relative values $\sigma_i = 0.1$ and 1 (Figure 8).

DISCUSSION

The frequency distribution of fish school diameters observed acoustically off the coast of southern California by Smith (1970) has a well defined most frequent, or peak, diameter. The distribution is also skewed towards small diameters and is relatively stable from one month's observations to the next. These data likely represent a range of fish sizes and species with northern anchovy probably being the dominant group.

The frequency distribution can be modeled by a probability equation that is based on a dynamic equation that contains deterministic and stochastic rates for the entrance and exit of fish from a school. The entrance rates are taken to be independent of the number of fish in a school while the exit rates are taken to be proportional to the number. The number of fish in a school is transformed to a diameter by assuming the average school shape is disklike so the number is proportional to the horizontal area, as expressed by the square of the diameter.

The effects of environmental conditions, fish sizes, species, predator-prey interactions, and stock size are assumed to be contained in the stochastic parameters of the dynamic equation. This assumption requires these basically unknown factors have white noise character.

In effect the deterministic behavior of the rate of change of diameter is represented by a dynamical equation, $dx/dt = f(x)$, where $f(x)$ is the deterministic rate and is a function of x. The remaining unknown fluctuating behavior, due to other factors, is approximated by $e(x)j(t)$ where $j(t)$ is white noise fluctuation and $e(x)$ gives the x dependence of the stochastic rate. Combining the rates we obtain a dynamical stochastic equation for x and the probability analysis of the process can be carried out using a Fokker-Planck equation, which is a diffusion equation for probability in x and t. The solution of the Fokker-Planck equation gives the probability curve $P(X)$.

Fitting the curve $P(X)$ to Smith's (1970) observations yields the equation constants or fitting parameters a, b, and c. These fitting parameters are ratios of the dynamic parameters of the dynamical stochastic equation for x.

The sensitivity analysis of $P(X)$ to relative changes in the dynamic parameters indicates two basic probability distributions can be produced: 1) a narrow probability distribution, favoring a narrow range of small diameters with the occurrence of large schools unlikely and 2) a wide distribution in which a wide range of larger diameters have low but essentially equal probabilities, and small diameters are unlikely. Wide distributions are favored by large entrance rates and a large amount of randomness to the schooling process. Narrow distributions are favored by large exit rates and low randomness in the schooling process. Additionally, wide distributions are favored for schools with a low fish density per cubic meter, and narrow distributions of diameters are favored with high density schools. The density of fish in schools is related to the fish length so the analysis infers that large fish should have a wide probability distribution of large diameters and small fish should develop a narrow probability distribution of small diameters.

From a commercial fishing viewpoint factors that affect school sizes are important and so, briefly, we consider a possible qualitative response of school diameter to fishing activity. If we envision the fishing process as an event that divides a school and removes one of the fractions, then we expect fishing should at least affect the deterministic parameters of the model. The dividing of the school, by fishing, decreases the mean time interval between school divisions and this, in turn, would increase the exit rate coefficient β. The fact that part of the stock is removed by fishing may increase the time interval between school encounters and thus decrease the entrance rate α. A con-

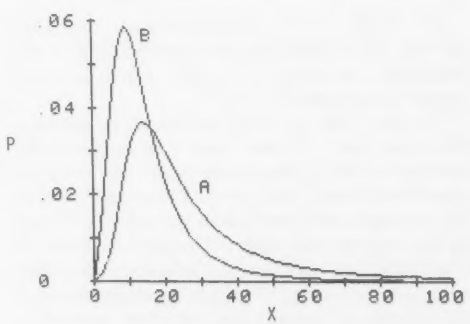

FIGURE 9.—Probability distribution (P) vs. school diameter (X) in meters. Curve A, distribution corresponding to Smith's (1970) observations. Curve B, distribution postulated for fishing activity that increases β and decreases α by 50%.

comitant increase in β and decrease in α would shift the probability distribution towards a narrow range of small diameters. For example, if we assume an increase in fishing activity off southern California decreases α and increases β by 50%, then there would be a noticable decrease in the occurrence of schools >20 m diameter (Figure 9).

ACKNOWLEDGMENT

I wish to thank Akira Okubo for his discussion on this problem.

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RECRUITMENT AND EXPLOITATION OF GULF MENHADEN, *BREVOORTIA PATRONUS*[1]

DEAN W. AHRENHOLZ[2]

ABSTRACT

Gulf menhaden, *Brevoortia patronus*, range along the Gulf of Mexico coast from Cape Sable, Florida, to Veracruz, Mexico, and are exploited by a purse seine fishery from Alabama to eastern Texas. Rates of exploitation, population movement, and recruitment into the fishery were estimated from returns of tagged juveniles and adults. The annual instantaneous rate of natural mortality (M = 1.0935) was estimated from recoveries of tagged adults. Recruitment patterns were determined and exploitation rates were estimated from returns of fish tagged as juveniles in specific geographic regions along the northern Gulf of Mexico. During 1971-73, fish tagged as juveniles from either the eastern or western extremes of the northern gulf coast were exploited as 1-year-olds at a mean rate of only 5%. The rate increased to a high of 51% for 1-year-olds tagged near the Mississippi Delta, the center of the fishery. During 1972-74, 2-year-old fish tagged as juveniles were exploited at rates ranging from 18 to 55%. Fish from the eastern and western ends of the range dispersed toward the center of the range as they grew older.

Gulf menhaden, *Brevoortia patronus*, range along the coastline of the Gulf of Mexico from Cape Sable, Fla., to Veracruz, Mex. (Reintjes 1969). They are exploited from April to October by a purse seine fishery that operates in nearshore waters from Alabama to Texas. Gulf menhaden move offshore in the fall before spawning in the winter. The larvae move into estuaries in late winter and spring, where they metamorphose into juveniles and remain there until the following autumn.

The fishery is dependent on age-1 and age-2 fish, with few fish being taken that exceed 3 yr of age. The catch, processed into meal and oil, increased from 8,900 t in 1946 to 728,500 t in 1971, and has fluctuated between 447,000 and 820,000 t since then. Yellowfin menhaden, *B. smithi*, and finescale menhaden, *B. gunteri*, occur in the area fished, but Gulf menhaden compose approximately 99% of the landings. At present, catches are processed at 11 reduction plants, located at six ports along coastal Louisiana and Mississippi (Figure 1). Large, refrigerated purse seine vessels, supported by spotter aircraft, range up to about 320 km from port. During recent years the number of operating plants has varied from 10 to 13, and the number of active ports has varied from 6 to 8 (Nicholson 1978).

To determine if fish reared outside the range of the fishery are exploited and to determine the rate of exploitation of individuals reared within the range, juvenile menhaden (young-of-the-year) have been tagged since 1970 in selected estuaries from Florida to the Mexican border. I analyzed returns from fish tagged as juveniles from 1970 to 1972 to determine if fish reared outside the range of the fishery contribute to landings and to estimate rates of exploitation by age and estuarine area of origin.

I also analyzed returns from a second (independent) adult tagging program to obtain an estimate of natural mortality and a preliminary estimate of rate of fishing on fully recruited fish to complement my analysis of the first (juvenile) tagging program. In the second study, reported by Pristas et al. (1976), Gulf menhaden were tagged as recruited fish (adults) on the fishing grounds from 1969 to 1971.

TAGGING METHODOLOGY

Since all tags that are recovered from both tagging programs are from "adult" fish caught by the fishery, a distinction in terminology is made in this paper for clarity in separating results: "tagged as adults" or "adult recoveries" refers to the study reported by Pristas et al. (1976) and "tagged as juveniles" or "juvenile recoveries" refers to the present study.

[1]Southeast Fisheries Center Contribution No. 81-31B.

[2]Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

Manuscript accepted September 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

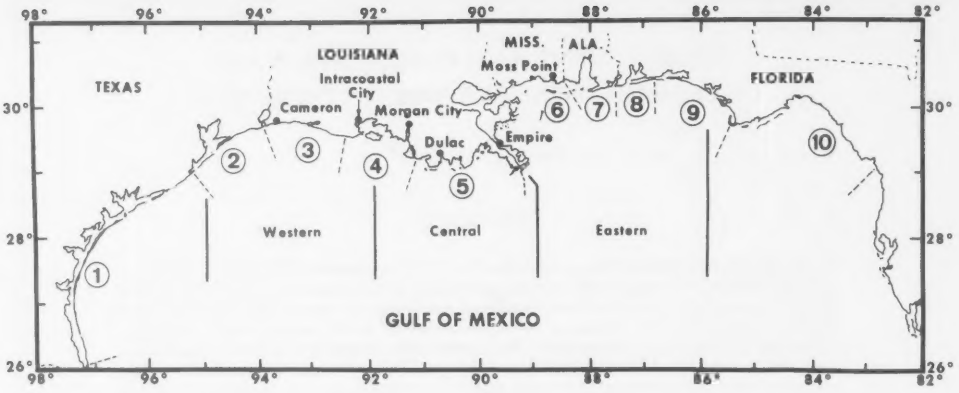

FIGURE 1.—Location of Gulf of Mexico ports where catches of Gulf menhaden are currently landed (dots), major fishing and tagged adult release areas (vertical lines), and division of the U.S. gulf coast into tagged juvenile Gulf menhaden release areas (numbered circles and dashes).

Methods of tagging and tag recovery are well documented (Pristas and Willis 1973; Parker 1973; Dryfoos et al. 1973). Numbered stainless steel ferromagnetic tags, 7.0 × 2.5 × 0.4 mm for juveniles, and 14.0 × 3.0 × 0.5 mm for adults, were injected into the body cavity. Juveniles were tagged in estuaries during late summer or early fall just before emigration. Adults obtained from fishing vessels on the fishing grounds were tagged during late spring.

Tags were recovered on magnets located in reduction plants; however, not all tags that entered a plant were recovered. To estimate the fraction of tags recovered at each plant, 100 tagged fish were put in the catch of a selected vessel each week. Field recoveries were adjusted for loss rates within a plant by multiplying the inverse of the test recovery fraction by the number of field tags actually recovered at each plant.

For analyzing juvenile tag recoveries, the northern Gulf of Mexico coast was divided into 10 release areas, numbered, and geographically named for reference (Figure 1, Table 1). In some areas, fish were tagged in only one estuary; in other areas, they were tagged in several estuaries. For analyzing adult tag recoveries, the coast was divided into three areas: western, central, and eastern (Pristas et al. 1976) (Figure 1).

TABLE 1.—Numbers of tagged juvenile Gulf menhaden released in estuarine waters by area and year, 1970-72. Areas are depicted in Figure 1.

Release area	1970	1971	1972
1. Southeast Texas	3,199	3,263	3,900
2. Galveston Bay	892	1,200	1,000
3. Western Louisiana	1,000	2,500	2,500
4. Central Louisiana	—	1,500	640
5. Western Delta	200	600	1,200
6. Eastern Delta-Mississippi	1,622	1,248	1,800
7. Mobile Bay	1,199	2,500	—
8. Pensacola Bay	600	1,000	1,700
9. Choctawhatchee Bay-St. Andrew Bay	—	200	2,482
10. Apalachee Bay	—	400	100
Total	8,712	14,411	15,322

MOVEMENT AND RECRUITMENT OF JUVENILE TAGGED FISH

The eventual distribution of fish tagged in specific estuaries would be an indication of the degree and direction of movement of fish from each estuary. Because there is no way of knowing exactly where a tagged fish was caught, and because levels of effort may vary between ports (and thus numbers of fish actually landed), the distributions must be inferred from estimates of the relative availability of tagged fish to each port rather than from just the distribution of recoveries of tagged fish to each port. Because vessels tend to fish more intensively in areas near their home ports, most tags recovered at a specific port were assumed to have been from fish caught in waters closest to that port. The measure of standardized effort (f') used in availability calculations is the vessel-ton-week (computed as net-registered-tonnage times number of weeks fished), the unit of fishing effort currently employed for this fishery (Chapoton 1972; Schaaf 1975), adjusted for differences in vessel catch efficiency in numbers of fish

between ports and between years. (Landing and effort data from a former plant at Sabine Pass, Tex., were combined with Cameron, La., data for 1971.) This adjustment, made by multiplying the actual effort by the ratio of actual catch per unit effort in numbers of individuals to the overall port's and year's mean catch per unit effort (in numbers), makes all measures of effort by port equivalent with respect to numbers of fish landed.

Relative availabilities were calculated for juveniles tagged in nine specific areas from 1970 to 1972. No tags were recovered from fish tagged in area 10, probably because so few were tagged. For each of six ports, the estimated number of tags recovered annually from fish tagged in specific areas was divided by the number of tags recovered at all ports over all years. The quotient was divided by the amount of standardized fishing effort for the port during the year considered, and a three-dimensional matrix of relative availabilities by age of capture, port, and year class was calculated for each release area. The equation used for these calculations is:

$$\overline{RAV}_{ijk} = (R_{ijk} / \sum_i \sum_j R_{..k}) / f'_{jm} \qquad (1)$$

where f'_{jm} = standardized effort,
R_{ijk} = number of recoveries, and
$\overline{RAV}_{ijk}$ = relative availability to a unit of effort.

Here, i refers to age at capture, j refers to port, k refers to year class, and $m = k + i$ (year captured).

The relative availability estimates at the different ports for each release area were similar between year classes and so were averaged for all years (Figure 2). These results support the hypothesis advanced by Kroger and Pristas (1975) that there is little or no exchange of fish between areas east and west of the Mississippi Delta. Large numbers of fish tagged east and west of the delta were recovered at Empire, La., plants; since vessels from these plants fish both sides of the delta there is no way of knowing on which side fish bearing these tags were actually captured. The few tags recovered at plants east of the delta of fish tagged west of the delta may actually have been taken by vessels from plants east of the delta fishing west of the delta, and vice versa. It is noteworthy that of the few tags recovered at plants west of the delta of fish tagged east of the delta nearly all were recovered at Morgan City and Dulac, La. Vessels from these ports were more likely to have fished east of the delta than were vessels from the two most western ports, Intracoastal City and Cameron, La. Almost no fish tagged east of the delta were recovered at these ports.

As fish age, there appears to be a slow dispersal toward the delta of fish from eastern and western areas. Fish tagged in the two most western areas were captured in greater numbers their second year after release at the two more central ports, Morgan City and Dulac. Although the fish tagged in the other three western areas were captured in greatest numbers their first year after release, they became progressively more available as 2-yr-olds to the three central ports than they were to the most western port at Cameron. However, 1-yr-old fish from these three western areas (3, 4, and 5) were disproportionately more available to the western extreme of the fishery than to the more central area. Fish tagged in the three most eastern areas were captured in greater numbers the second year after release at the Moss Point, Miss., and Empire plants. Fish tagged in the eastern area adjacent to Moss Point, although captured in greater numbers the first year after release, appeared to be more available as 2-yr-olds to Empire vessels than to Moss Point vessels.

As a consequence of the fishery being concentrated in Mississippi and Louisiana waters, fish reared as juveniles in the extreme eastern (Alabama and Florida) and western portions (Texas to the Mexican border) of the range are recruited at a lesser rate than fish reared in the center of the range. Fish moving toward the center of the range probably are recruited progressively later in the season as age 1, and many may not be recruited until age 2, whereas nearly all fish reared in the center of the range probably are recruited early in the season at age 1.

The gradual shift toward the center of the fishing area as a year class ages, indicated by the pattern of juvenile tag recoveries, is also indicated by the age composition of the catches. Age-1 fish compose a higher percentage of catches at plants or longitudes at the eastern and western ends than at plants or longitudes in the center (Nicholson 1978). The observed age composition is not due to greater fishing pressure on fish at either end of the fishing grounds, since attrition rates of fish tagged in the more central areas, implied by catch curves of tag recoveries, are equal to or greater than rates observed for fish tagged in either extreme (Figure 3). This shifting is apparently superimposed over

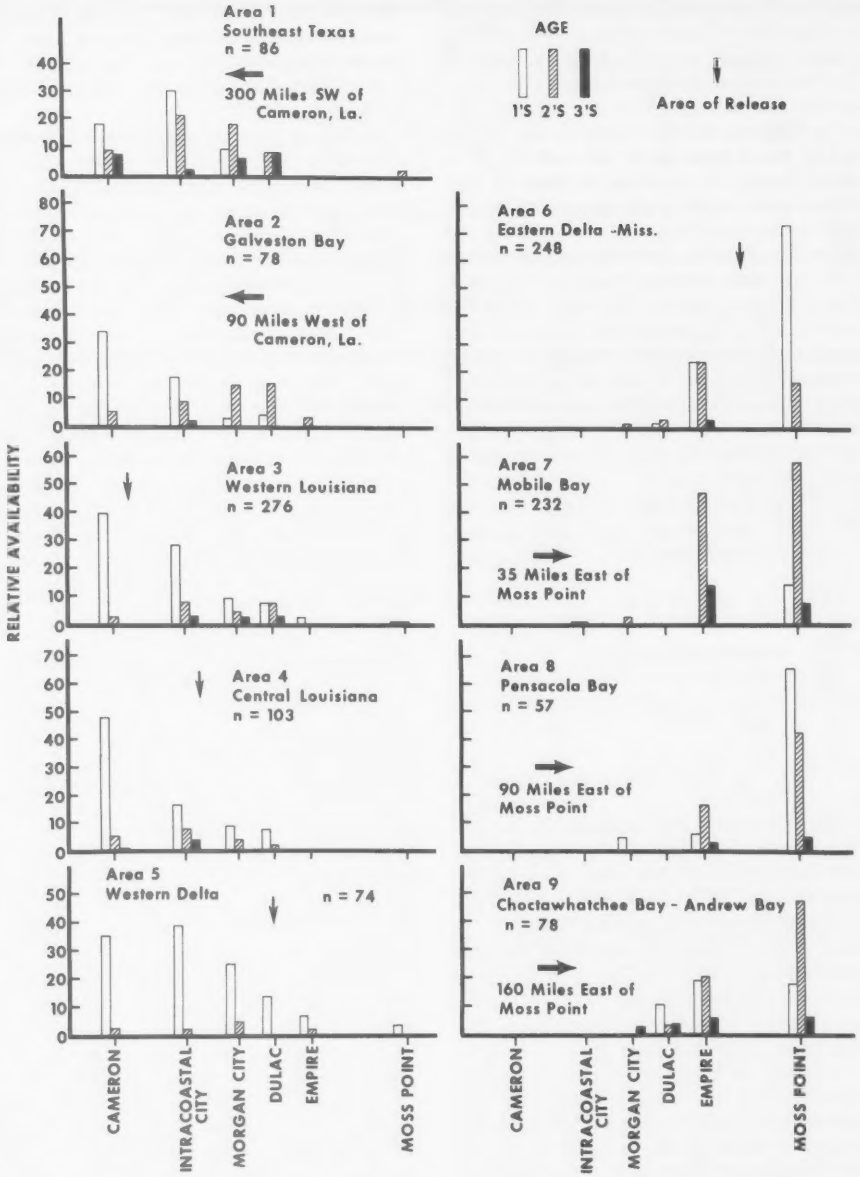

FIGURE 2.—The mean release area-specific availability by age of Gulf menhaden tagged as juveniles to individual ports in the Gulf of Mexico. Vertical arrows denote approximate release location with respect to the ports, horizontal arrows denote release locations beyond the range of the figure. The actual (unadjusted) number of tag returns is given for each release area.

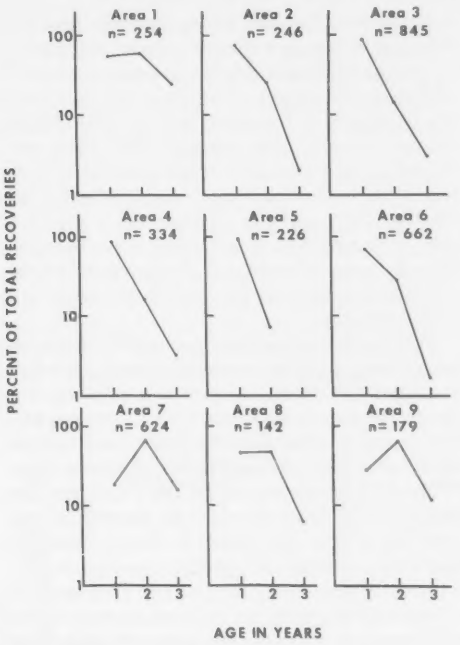

FIGURE 3.—The frequency of recoveries for a standard 100 tags for each juvenile Gulf menhaden release area (ordinate logarithmically scaled) and the adjusted number of recoveries from each release area, Gulf of Mexico.

an annual fall-spring, offshore-onshore migration (Roithmayr and Waller 1963).

The lack of precise recapture location information and the limited range of the fishery relative to the range of the species prevents the formulation of a more detailed and possibly more accurate description of dispersal patterns of Gulf menhaden. For instance, it is possible that fish from nursery areas outside the fishing grounds disperse at a more or less equal rate towards and away from the fishery. However, the relatively strong showing of tags from outside the fishery 2 and 3 yr after release and the relatively few schools of Gulf menhaden that are sighted at the extremes of the range indicate that dispersal is probably stronger towards the center of the range, where the fishery is heaviest, rather than away from it.

MORTALITY RATE ESTIMATION FROM ADULT TAG RECOVERIES

To estimate the age specific exploitation rate of Gulf menhaden from different geographic nursery areas, I needed an estimate of the instantaneous natural mortality rate (M) and an estimate of the exploitation rate (u) of fully recruited fish. I used the tag recovery data from the adult tagging study reported by Pristas et al. (1976) to estimate these parameters, because these fish (being obtained from commercial purse seine sets) were assumed to be fully recruited when tagged, and the adult tagging study is independent from the juvenile tagging study which will be used as the data base for the area and age specific exploitation estimation. Before mortality rates were estimated, however, adjustments were made to the adult tag-recovery data to remove the potential for systematic errors in the results.

A, B, and C errors (Ricker 1975) are commonly associated with tagging studies attempting to estimate rates of survival and fishing. Type A errors can occur when tagged fish die as a result of marking or shed their tag shortly after tagging and also during the recovery phase when reporting of recoveries is incomplete (in this case loss of tags within a reduction plant). Type A errors are characterized by affecting estimates of rate of fishing (hence rate of natural mortality) but not rates of total mortality when these parameters are estimated by rates of recovery over several time intervals.

Adjustments of numbers recovered for incomplete recovery of tags from harvested tagged fish is straightforward and is outlined in the Tagging Methodology section. Adjustments of numbers released entailed adjusting for any significant difference in recovery rates associated with different taggers and then determining a realistic estimate of rate of loss due to death and shedding shortly after tagging, which is applicable to all taggers. Since only three taggers were employed in this study, and one only tagged 200 fish in 1971, a recovery comparison was conducted between the two taggers who tagged the greatest number (99.7%) of the fish. Because the recovery rate for fish tagged by one individual (tagger B) was much lower than the rate for fish tagged at the same time by the other (tagger A) (Table 2), the number of tags applied during 1969 by this tagger was adjusted downward. The adjustment was made by multiplying tagger B's number released for each area by the ratio of the recovery rate of tagger B to tagger A for each area. All of the remaining releases (1970 and 1971, with the exception already noted above) were tagged by tagger A. Adjusted recov-

TABLE 2.—Comparison of differences in recovery rates between taggers for paired tagging of adult Gulf menhaden conducted in 1969 in the Gulf of Mexico. All chi-square values obtained from 2×2 contingency tables were highly significiant ($P<0.001$).

Area	Tagger	No. tagged	Actual recoveries	Chi-square
Eastern	A	6,700	1,118	77.05
	B	6,300	713	
Central	A	1,900	402	36.54
	B	1,800	245	
Western[1]	A	4,100	456	120.04
	B	3,700	163	

[1]Release totals in Table 3 contain an additional 2,500 tags released by tagger A working alone.

eries and numbers released with adjustments for differential tagger induced mortality (1969 only) for the adult study are given in Table 3. (The number of adjusted recoveries differs from the number published by Pristas et al. (1976), probably because slightly different methods were used to adjust known recoveries and somewhat different criteria were used to judge the suitability of some returns.)

Adjustments of numbers released to account for tags lost from initial mortality and shedding had to be somewhat arbitrary. Kroger and Dryfoos (1972) reported on a series of short-term tagging mortality and shedding studies on Atlantic menhaden, *B. tyrannus*, which tested a variety of methods of insertion, fish size, chemical treatment of tags, and tag size. Of this series, two were with fish size and tagging methodology similar to the Gulf adult study. Losses due to mortality and initial shedding in these two experiments were 10 and 24%. Since these experiments were conducted under better conditions than field tagging, I selected a value nearer the higher of the two estimates, 20%, as a realistic mean rate of Type A tag loss, and 10-30% as a range for testing the sensitivity of this assumption.

Type B errors can occur when tags are shed throughout the recovery period, when tagged fish have a higher rate of mortality, or when tagged fish emigrate from the fishing grounds. Errors of this type will cause overestimation of total mortality and natural mortality but not necessarily rate of fishing. No corrections were made for Type B errors because no long-term studies of shedding or mortality under this category have been conducted with menhaden. Since tagging wounds heal within a few weeks after tagging (Kroger and Dryfoos 1972) and the internal tag is stainless steel with rounded, smooth edges, I would expect Type B losses to be minimal. Emigration from the fishing grounds is unlikely (see Recruitment section above).

Type C errors occur when the tagged individuals are either more or less susceptible to capture than untagged fish during the first year after release. Recovery rates for later years may be representative, however. Adjustment for Type C error is made in the estimating method, as will be shown later.

The Gulf menhaden tag-recovery data are subject to an additional type of error. Sometimes tags from recaptured fish lodged in plant machinery and were not recovered until 1 or more years after entering a reduction plant (Table 4). The retention of tags in plants for more than one season prior to their recovery will cause estimates of total mortality to be too low. Since trial calculations (of simulated data) showed that the rates of tag retention noted would cause underestimation by only about 5.4% for fish marked with large (adult) tags and 3.8% for fish marked with small (juvenile) tags, and attempts to adjust for this bias may introduce additional error, the effects were ignored. [Tag retention rates were not as large as reported by Nicholson and Schaaf (1978). The most serious discrepencies were for two plants during 1972, where retention rates were reported as 5 and 6%. It was discovered that 34 of the 59 tags reported as retained for 1 yr in one plant and 92 of the 93 tags reported as retained in the other plant were erroneously recorded. Corrected retention rates are 2 and <0.1% for the two plants.]

Plots of log frequencies of adult recoveries for each release year and area (Table 3) on years-at-

TABLE 3.—Number of adult Gulf menhaden tagged in late spring, by area, year, and adjusted number recovered, Gulf of Mexico.

			No. recovered in year			
Area	Year	No. tagged	1	2	3	4
Western Gulf	1969	[1]8,065	1,363	509	68	6
	1970	9,100	3,619	838	15	4
	1971	7,400	2,622	235	24	1
Central Gulf	1969	[1]3,056	1,311	215	21	—
	1970	5,100	2,168	408	22	—
	1971	5,200	1,617	94	11	6
Eastern Gulf	1969	[1]10,965	2,305	1,123	134	22
	1970	3,575	1,315	321	33	7
	1971	10,200	2,694	742	89	9

[1]Adjusted for tagger induced mortality.

TABLE 4.—Mean percentage of large (adult) and small (juvenile) test tags recovered in Gulf menhaden reduction plants, Gulf of Mexico.

Tag type	Release years	Percentage recovered in season of release	Percentage recovered in seasons after release		
			1st	2d	3d
Large	1969-71	51	0.56	0.05	0.02
Small	1970-72	34	.38	.02	.01

large indicate that mortality rates were generally similar for all areas and years (Figure 4). Since not all areas and years had 4 yr of recoveries, and two of the three areas did not have strongly linear plots (hence a constant annual Z) for 1970 releases, I selected the more linear 3 yr of recovery data from each area for 1969 and 1971 for further analysis (points joined by solid lines on Figure 4). Based on the plotted data of Figure 4, I assumed that Z (hence survival and rate of fishing) was constant for years 1-3 following release for the western area in 1971 and the central area in 1969 and 1971. I assumed a Type C error condition for the first year after release for the western area in 1969 and the eastern area in 1969 and 1971 and assumed Z to be constant for years 2-4 in these three data sets. I also assumed that all the fish tagged as adults, which were released in late spring just after fishing had begun, were subjected to a full season of natural mortality.

I used the slope of a weighted regression of the natural logarithms of recoveries on years-at-large where mortality was assumed constant as an estimate of Z. Each regression point was weighted by the number of unadjusted recoveries that provided the basis for that point.

For release groups with an estimate of constant Z for years 1-3, called here Z_1, the constant annual exploitation rate (u_1) was estimated directly by (Ricker 1975):

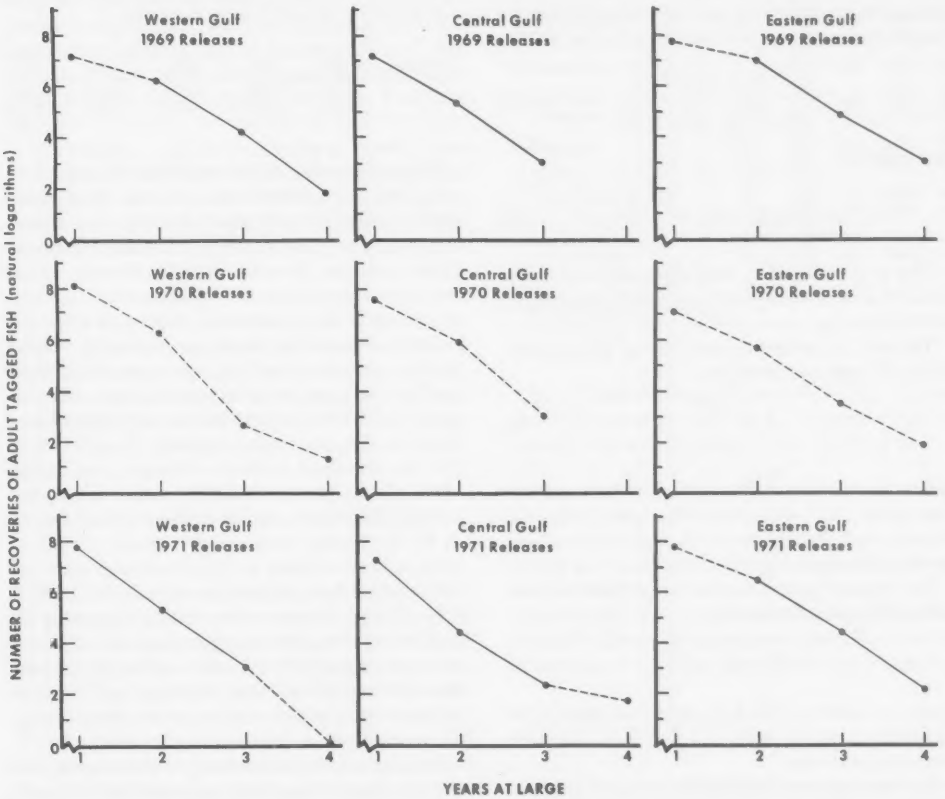

FIGURE 4.—Natural log frequency of recoveries by years at large for tagged adult Gulf menhaden by fishing area and release year, Gulf of Mexico. Lines connect points used to estimate instantaneous total mortality rate (Z) (assumed constant for 3 consecutive years), and dashes connect points not used in the estimation procedure for Z.

$$u_1 = \frac{R_1 + R_2 + R_3}{M'(1 + S_1 + S_1^2)} \quad (2)$$

where M' = the number tagged and released, adjusted for tagging loss,
$S_1 = e^{-z}$, the constant annual survival rate, and
R_n = number of adjusted recoveries for years-at-large n.

For release groups with an estimate of constant Z for years 2-4, called here Z_2, the constant exploitation rate (u_2) had to be estimated by trial, since the rate for the first season could not be assumed a constant for later years (Type C error condition). A trial value of Z_1 for the first year-at-large also provided first year trial values of S_1 and A_1 (total annual mortality rate); u_2 was estimated for the second and later years-at-large by (Ricker 1975):

$$u_2 = \frac{R_2 + R_3 + R_4}{S_1 M'(1 + S_2 + S_2^2)} \quad (3)$$

and also by:

$$u_2 = \frac{A_2}{Z_2}\left(Z_2 - Z_1 + \frac{R_1 Z_1}{M' A_1}\right). \quad (4)$$

The trial value of Z_1 was adjusted until Equations (3) and (4) converged on virtually equivalent estimates of u_2.

The annual instantaneous rate of fishing mortality (F) was estimated by:

$$F = \frac{uZ}{A} \quad (5)$$

where $A = 1 - e^{-z}$, the total annual mortality rate, and u, Z, F, and A are subscripted 1, where Z was constant through years 1-3, and 2 where Z was constant through years 2-4.

The annual instantaneous rate of natural mortality (M) was estimated by:

$$M = Z - F \quad (6)$$

where, as above, Z and F are subscripted 1 for constant mortality years 1-3 and 2 for constant mortality years 2-4.

The central area had the greatest variation in parameter estimates between years, while the western area had the least (Table 5). I averaged all estimates of M and u for each tagging loss rate examined to obtain unweighted means (Table 6). A change in the estimate of tagging loss resulted in a slightly greater than 1:1 fractional change in the estimates of M and u.

TABLE 5.—Estimated annual instantaneous natural (M) and fishing (F) mortality rates and exploitation rates (u) for tagged adult Gulf menhaden in the Gulf of Mexico, assuming a 20% initial tag loss to shedding and mortality.

Area	Year	M	F_1	F_2	u_1	u_2
Western Gulf	1969	1.1672	—	0.9300	—	0.3890
	1971	1.2287	1.1665	—	0.4426	—
Central Gulf	1969	.6927	1.2043	—	.5396	—
	1971	1.6083	1.1367	—	.3875	—
Eastern Gulf	1969	.8805	—	1.1673	—	.4965
	1971	.9835	—	1.1662	—	.4793

TABLE 6.—Estimates of mean annual rate of exploitation (u) and instantaneous natural mortality rate (M) for Gulf menhaden in the Gulf of Mexico, estimated from recoveries of tagged adults, with varied levels of tagging mortality.

Parameter	Tagging loss rate				
	10%	15%	20%	25%	30%
u	0.4122	0.4328	0.4558	0.4815	0.5106
M	1.2019	1.1506	1.0935	1.0293	0.9568

Since the earlier estimates of each Z were from weighted regressions with only three data points and hence only one degree of freedom for estimating confidence intervals (C.I.), I conducted a combined analysis of scaled data for the six sets of release-recovery data for 1969 and 1971 (which consist of 18 data points and, hence, 16 df) to determine the stability of the estimate of M relative to the variance about the estimate of Z. After scaling the data, each release-recovery set summing to 10,000, I estimated the unweighted predictive regression slope estimate of Z_2 and its 95% C.I. by standard methods (Draper and Smith 1966). Assumptions on which years represented periods of constant total mortality were the same as for the earlier analysis. Equations (3) and (4) were used to estimate u_2 from the scaled estimate of Z_2 and for the high and low extremes of the 95% C.I. F_2 and M were estimated by Equations (5) and (6) as before. The resulting estimate of M and its approximate 95% C.I., although slightly lower than the earlier estimate, represent very similar values, and relative to the variance about the estimate of Z_2, M is quite stable (Table 7).

To determine if the arbitrary selection of 3 yr of recovery data for analysis, adjustment for Type C error, and use of weighted regressions had a major altering effect on the resulting estimate of M, I estimated M using all recovery data points for the

TABLE 7.—Estimates from scaled data of total annual instantaneous mortality rate (Z_2), rate of exploitation (u_2), instantaneous fishing mortality (F_2), instantaneous natural mortality (M), and their approximate 95% confidence intervals (C.I.), for Gulf menhaden tagged as adults in the Gulf of Mexico.

Parameter	Estimate	High 95% C.I. limit	Low 95% C.I. limit
Z_2	2.2241	2.4356	2.0126
u_2	0.4692	0.5041	0.4307
F_2	1.1701	1.3456	1.0005
M	1.0540	1.0900	1.0121

1969 and 1971 releases, no Type C correction, and an unweighted predictive regression estimate for Z. The resulting mean estimate for M, 1.0852, is very similar to the estimate of M, 1.0935, obtained from the more refined analysis. Inclusion of the 1970 release-recovery data in this analysis resulted in a somewhat lower mean estimate of M, 1.0089. The lower M estimates for the 1970 releases probably resulted from a lower rate of tagger induced mortality than for the 1969 and 1971 release groups, as the 1970 tagged fish were larger than the fish tagged during the other 2 release years.

As evidenced by the similarity of results from the two modified analyses and the results depicted in Table 6, the estimate of M is apparently more sensitive to the correction factor for tagging mortality loss than the estimates of other parameters used in its estimation. Unfortunately, data on the nature of the statistical distribution on which to base variance estimates and hence approximate 95% C.I. are lacking. Based on the current knowledge of tagging mortality for menhaden, the estimates obtained for a 20% tagging loss and the weighted regression technique ($M = 1.0935$ and $u = 0.456$) are the best estimates currently available.

AREA-SPECIFIC AND AGE-SPECIFIC EXPLOITATION RATES

To estimate area-specific and age-specific exploitation rates from recoveries of tagged juveniles, it is necessary to estimate the number of tagged fish alive at the beginning of each fishing season. These numbers can be estimated from the number of recoveries by sequential analysis (Ricker 1975). The data and parameters needed are the number of recoveries (R_n) by age (n), an estimate of M, and an estimate of u for a given cohort during its last year in the fishery.

The numbers of tags recovered in all years for fish released in specific areas were pooled by age of capture and, with one exception, were unweighted (Table 8). For three estuaries, which constituted the southeast Texas area, the recoveries were weighted so that each estuary contributed equally to the totals.

TABLE 8.—Area-specific annual exploitation and fishing mortality rates estimated by sequential analysis of recoveries of tagged juvenile Gulf menhaden in the Gulf of Mexico. Numbers in parentheses are initial rates of exploitation obtained from the analysis of adult-tagged fish.

Area	Age	N_n	u	F	S	R_n
1. Southeast Texas[1]	1	2,557	0.050	0.086	0.3074	129
	2	786	.184	.348	.2366	145
	3	186	(.456)			85
2. Galveston Bay	1	656	.270	.549	.1935	177
	2	127	.505	1.351	.0868	65
	3	11	(.456)			[2]5
3. Western Louisiana	1	2,096	.338	.737	.1603	709
	2	336	.330	.715	.1639	111
	3	55	(.456)			25
4. Central Louisiana	1	763	.373	.843	.1442	284
	2	110	.390	.901	.1361	43
	3	15	(.456)			7
5. Western Delta	1	412	.509	1.373	.0849	210
	2	35	(.456)			16
6. Eastern Delta-Mississippi	1	1,748	.265	.538	.1956	464
	2	342	.547	1.563	.0702	187
	3	24	(.456)			11
7. Mobile Bay[3]	1	3,896	.027	.045	.3203	105
	2	1,248	.343	.753	.1578	429
	3	197	(.456)			90
8. Pensacola Bay	1	587	.112	.200	.2743	66
	2	161	.417	.992	.1242	67
	3	20	(.456)			9
9. Choctawhatchee Bay-St. Andrew Bay	1	977	.049	.084	.3080	48
	2	301	.368	.830	.1461	111
	3	44	(.456)			20

[1]Weighted recoveries for this subarea only.
[2]Pooled age-3 and age-4 recoveries.
[3]Estimates are unrealistic; see Table 9 and text.

The number of tagged fish alive (N_n) in their last representative year in the fishery at the beginning of a fishing season was estimated by:

$$N_n = \frac{R_n}{u} \tag{7}$$

where $u = 0.456$ from the adult tagging analysis.

An estimate of S_{n-1} was required to estimate the number of 2-yr-old tagged fish alive (N_{n-1}) at the beginning of a fishing season from the equation:

$$N_{n-1} = \frac{N_n}{S_{n-1}}. \tag{8}$$

S_{n-1} was estimated by substituting trial mortality estimates (assuming $M = 1.0935$) into the following equation until the right side equaled the number of recoveries at age $n - 1$ (Ricker 1975):

$$R_{n-1} = N_n \left[\frac{F_{n-1} A_{n-1}}{S_{n-1} Z_{n-1}} \right]. \quad (9)$$

By repeating this procedure, Equations (9) and (8), using N_{n-1} as an estimate of 2-yr-olds alive at the beginning of a fishing season, the number of tagged 1-yr-olds (N_{n-2}) alive at the beginning of a fishing season was estimated.

Age (n) specific exploitation rates were estimated for each release area by using the estimated age specific mortality rates in:

$$u_n = \frac{F_n A_n}{Z_n}. \quad (10)$$

Except for fish tagged in the Mobile Bay, Ala., area (Alabama coastal waters are closed to purse seining) the exploitation rates for both age-1 and age-2 fish declined progressively as the distance from the delta increased. The decline was much greater for age-1 than for age-2 fish (Figure 5). The low rates of entry of fish from the extremes of the range and the purse seine closure imposed for coastal Alabama waters may enable a small buffer stock to survive in the event of heavy exploitation.

For fish tagged in Mobile Bay, the number estimated to have been alive at the beginning of the first fishing season exceeded the number of fish tagged, an obvious impossibility (Table 8). In outside waters, Gulf menhaden are taken incidentally by the industrial bottom trawl fishery (Roithmayr and Waller 1963) and by the shrimp fishery in inside and outside waters. The overestimate of N_1 may have been the result of estimated M being too high for this group of fish. One possibility for M being too high is that the loss of tagged fish to other causes, which is included in the estimate of M, may be lower than for fish tagged in all other areas.

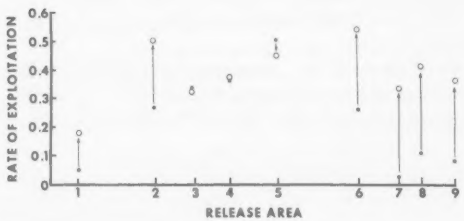

FIGURE 5.—The rate of exploitation by release area for age-1 (dots) and age-2 (circles) Gulf menhaden tagged as juveniles in estuaries on the Gulf of Mexico. Arrows indicate degree and direction of change between years.

Estimates of initial tag loss from shedding and death were made by comparing the number of fish estimated to have been alive at the beginning of the first season with the number that should have been alive if only natural mortality ($M = 1.0935$) had caused deaths during the approximately 8 mo (0.67 yr) following tagging. The apparent tagging loss estimates (L) were calculated by estimating the fraction by which M' would have to be reduced to equal N_1 prior to undergoing 8 mo of natural mortality, i.e.:

$$(M' - LM')e^{-0.67M} = N_1$$

by solving for L and simplifying,

$$L = 1 - \frac{N_1}{M'(e^{-0.67M})}. \quad (11)$$

The resulting estimates, expressed as a percentage of the number of fish tagged, ranged from 22.1 to 63.0% (Table 9). These estimates seemed realistic in view of the loss rates reported by Kroger and Dryfoos (1972) for Atlantic menhaden of similar size tagged with small (juvenile) tags. These estimates do not, however, have any bearing on the 20% tagging loss estimate used for the adult study, as this study used larger fish and larger tags.

TABLE 9.—Numbers of juvenile Gulf menhaden tagged in autumn, numbers estimated by sequential analysis to have been alive the following April, and effectual tagging loss rates, Gulf of Mexico.

Release area	Number tagged	Number estimated alive	Effectual tagging loss
1. Southeast Texas[1]	13,460	2,557	0.605
2. Galveston Bay	3,092	656	0.559
3. Western Louisiana	6,000	2,096	0.273
4. Central Louisiana	2,140	763	0.258
5. Western Delta	2,000	412	0.571
6. Eastern Delta-Mississippi	4,670	1,748	0.221
7. Mobile Bay[2]	3,699	3,896	—
8. Pensacola Bay	3,300	587	0.630
9. Choctawhatchee Bay-St. Andrew Bay	2,682	977	0.242

[1]Weighted data for this area only.
[2]Unrealistic results, see text.

ACKNOWLEDGMENTS

Thanks are due to the many past and present employees of the Southeast Fisheries Center Beaufort Laboratory, NMFS, NOAA, who were involved in the many aspects of the menhaden

tagging programs. I am grateful to Eldon J. Levi, Donnie L. Dudley, James F. Guthrie, and Charles W. Krouse for assistance in editing and compiling tag release-recovery data and to Rober B. Chapoton, Charles S. Manooch III, William R. Nicholson, John W. Reintjes, and William E. Schaaf for critically reviewing this manuscript during various stages of preparation. I am indebted to Walter R. Nelson for critically reviewing the manuscript and providing encouragement during this study.

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NATURAL STABLE CARBON ISOTOPE TAG TRACES TEXAS SHRIMP MIGRATIONS[1]

BRIAN FRY[2]

ABSTRACT

A 1978 spring and early summer survey of Texas brown shrimp, *Penaeus aztecus*, showed that stable carbon isotope ($^{13}C/^{12}C$ or $\delta^{13}C$) analysis is useful for tracing shrimp movements. At least four isotopically distinct shrimp feeding grounds (three estuarine and one offshore) exist along the Texas coast. Mean $\delta^{13}C$ values for brown shrimp in these feeding grounds during the spring and early summer were −12.8 to −15.4 (sea grass meadows), −16.2 to −16.8 (offshore), −17.9 to −19.6 (open bays, group 1), and −20.1 to −21.7 (open bays, group 2). Longer term seasonal studies offshore and at two sea grass stations showed that shrimp $\delta^{13}C$ values become less negative by 1.2 to 2.4‰ in the fall versus spring/early summer. Many small subadult brown shrimp collected offshore and during outgoing tides in a channel leading to the offshore Gulf of Mexico had $\delta^{13}C$ values typical of individuals in sea grass meadows. These and possibly other shallow-water habitats appear to supply more shrimp to south Texas offshore fisheries than do deeper estuarine bays.

Migratory movements of many commercial marine species are difficult to follow. Traditional methods include mark-recapture techniques to follow individual growth and movement while sequential trawling studies follow mass migrations. Newer techniques based on underwater acoustics or genetic differences among stocks have expanded our ability to follow marine migrations, but many movement patterns remain unresolved.

Recently, the study of stable carbon isotope ratios, $^{13}C/^{12}C$ or $\delta^{13}C$, has shown that animals acquire a natural isotopic label or tag from their diet. The carbon in animals is generally isotopically similar within a range of ±2‰ to the carbon in the diet (DeNiro and Epstein 1978; Fry et al. 1978; Teeri and Scholler 1979). Photosynthesis introduces $\delta^{13}C$ variations among different plant species (Park and Epstein 1960; Smith and Epstein 1971), and the $\delta^{13}C$ values of animals may be interpreted in terms of the relative carbon contributions from plants at the base of food chains. In the Gulf of Mexico, marine sea grass species have the least negative $\delta^{13}C$ values (−3 to −15‰) while phytoplankton and particulate organic carbon are usually more negative (−18 to −25) and other species of marine algae are intermediate (−12 to −20) (Craig 1953; Parker 1964; Smith and Epstein 1971; Eadie and Jeffrey 1973; Fry and Parker 1979). Animals in sea grass meadows are usually less negative than animals found offshore, reflecting the general $\delta^{13}C$ difference between sea grass plants and phytoplankton (Parker and Calder 1970; Thayer et al. 1978; Fry and Parker 1979; McConnaughey and McRoy 1979).

This study assesses the potential of using $\delta^{13}C$ variations to trace shrimp movements. Since food availability differs between habitats such as sea grass meadows and phytoplankton-dominated open bays, the $\delta^{13}C$ label acquired during feeding will differ between such habitats. Measuring the $\delta^{13}C$ values of migrating shrimp should provide an indication of which habitats they came from and a basis for evaluating which habitats are relatively important numerical contributors to commercial shrimp fisheries.

During 1978, I analyzed the $\delta^{13}C$ values of the migratory brown shrimp, *Penaeus aztecus*, and to a lesser extent, of the pink shrimp, *P. duorarum*. These shrimp share a similar life history pattern of offshore spawning, juvenile growth in estuaries, subsequent offshore migration of subadults, and final maturation to adults that spawn offshore (Cook and Lindner 1970). Several nonmigratory shrimp and one offshore stomatopod species were also collected to facilitate interpretation of $\delta^{13}C$ patterns as due to local conditions vs. migration. Seasonal studies assessed the rate at which local food variations cause a change in shrimp $\delta^{13}C$.

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Manuscript accepted September 1980.
FISHERY BULLETIN: VOL. 79, NO. 2, 1981.

METHODS

Shrimp samples were collected at 22 bay and 3 offshore stations along the Texas coast (Figure 1). Most bay sampling was done by the Texas Parks and Wildlife Department, Coastal Fisheries Division, as part of their 1978 spring shrimp survey. Depths at bay stations were 1-2 m; offshore trawling areas were located in 27-29 m depths. Open bay stations had unvegetated mud bottoms and were not within 0.25 km of a major swamp, sea grass meadow, or marsh. Sea grass stations were all in or on the edge of large sea grass meadows measuring at least 5 ha.

Four open bay stations deserve individual mention. Clear Lake (station 100) and the old Arroyo Colorado (station 13) receive substantial amounts of domestic sewage. Station 94, at the mouth of the Tres Palacios River, had the lowest salinities of any station. Station 92 in Turtle Bay was in the open bay, but well-developed *Spartina* sp. marshes were present on the shore.

Shrimp were collected either with bar seines or trawls and then frozen in seawater for later identification and $\delta^{13}C$ analysis. Surface temperature and salinity were measured at the time of collection. Spring samples were mostly collected during a 6-wk period from mid-April to 1 June 1978. Offshore samples were collected 26 July 1978.

White muscle tissue was dissected from shrimp abdomens for $\delta^{13}C$ analysis. Both composite and individual samples were prepared. Composite samples contained equal-weight tissues from individual shrimp. Preliminary analysis of the number of pooled brown shrimp required for an accurate estimate of mean shrimp $\delta^{13}C$ showed that combining five or six individuals is generally sufficient (Figure 2); accordingly, composite sample sizes were ≥10 for all shrimp, and averaged 34 individuals/sample. For individual shrimp, mus-

FIGURE 1.—Shrimp collection stations in the northwestern Gulf of Mexico.

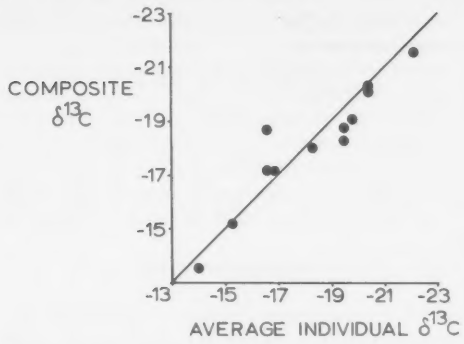

FIGURE 2.—Agreement between two methods of estimating mean shrimp $\delta^{13}C$ at 12 bay stations. The mean $\delta^{13}C$ value of five or six individuals is plotted as the x coordinate; the $\delta^{13}C$ value of the composite sample from which the individuals were subsampled is plotted as the y coordinate. The 45° reference line indicates complete agreement between the two methods.

cle tissue taken from the same shrimp showed a maximum $\delta^{13}C$ range of 0.3‰ (three shrimp, each sampled thrice), and subsampling one piece of tissue per shrimp was therefore considered adequate.

Shrimp were sorted by species by hand, and identification checked with a dissecting microscope on 5-10 specimens per composite sample using several keys (Zamora and Trent 1968; Pérez-Farfante 1970; Wood 1974).

Composite and individual samples were dried in an oven or freeze dryer, then shredded through a #40-mesh screen with a Thomas-Wiley Mill[3] or ground to a fine powder with mortar and pestle. Samples were combusted in a modified Leco radio frequency furnace (Parker et al. 1972) and analyzed for $\delta^{13}C$ values using a Nuclide 6-60 dual collector isotope ratio mass spectrometer. All results are expressed relative to the international PDB[4] standard where:

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \right) \times 10^3.$$

Based on analysis of 53 paired replicate samples, the mean error ±95% confidence limits was 0.45±0.77‰.

RESULTS

Bay Shrimp

Figure 3 shows the $\delta^{13}C$ values of brown shrimp from all bay stations sampled during the spring and early summer. The sampling effort was unequal at these stations, primarily due to fluctuations in shrimp numbers from week to week. At most stations, three or more composite samples were collected at irregular intervals over the 2-mo period; individual subsamples of pooled composite samples were collected between 1 and 15 May.

Analysis of variance showed highly significant differences between station means computed from composite samples ($P<0.01$). The LSD multiple range test showed that bay stations formed at least three significantly different groups on the basis of their mean $\delta^{13}C$ values (Figure 3; vertical bars at right margin). Most stations were open bay stations and had mean $\delta^{13}C$ values between −17.9 and −19.6‰ (stations 60-84). Mean $\delta^{13}C$ values were higher in sea grass meadows, −12.8 to −15.4‰. Several open bay stations formed a third group, having more negative average values of −20.1 to −21.7‰ (stations 80-13).

Analysis of the open bay stations showed that the more negative shrimp $\delta^{13}C$ values tended to occur in lower salinity bays which have been historically well flushed by freshwater inflows (Table 1).

TABLE 1.—Brown shrimp $\delta^{13}C$ and salinity at open bay stations and freshwater flushing rates for five Texas bays and the Gulf of Mexico.

Bay	$\delta^{13}C$[1] mean±SD(*N*)	Salinity[2] mean±SD(*N*)	Mean bay turnover rates (times/yr)[3] Historical	1951-68
Galveston	−20.0±0.9(19)	20.2±2.5(24)	3.9	3.1
San Antonio/ Espiritu Santo	−19.2±1.1(17)	16.7±4.8(25)	2.6	2.2
Matagorda	−18.3±1.3(17)	20.9±5.0(25)	1.3	1.3
Copano/Aransas	−17.7±0.6(9)	22.5±2.2(30)	.2	.2
Laguna Madre[4]	−17.6±0.6(2)	32.0±4.4(3)	.02	.02
Offshore, July	−16.5±0.6(15)	≈36	≈0	≈0

[1]Based on composite samples only.
[2]Salinity taken at the time of shrimp collection (mid-April to mid-June 1978).
[3]Turnover rate is the ratio of annual freshwater inflow volume to the volume of a bay. Calculated from Table 8, Diener 1975.
[4]Station 13 in the Old Arroyo Colorado is not included in this average.

Size and Bay Brown Shrimp $\delta^{13}C$

Systematic $\delta^{13}C$ changes with size might be expected if shrimp foods available to different size classes possessed different $\delta^{13}C$ values. Shrimp sizes ranged from 20 to 110 mm total length (TL),

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
[4]Abbreviation in the isotopic literature for a fossil belemnite, *Belemnitella americana*, from the PeeDee formation in South Carolina.

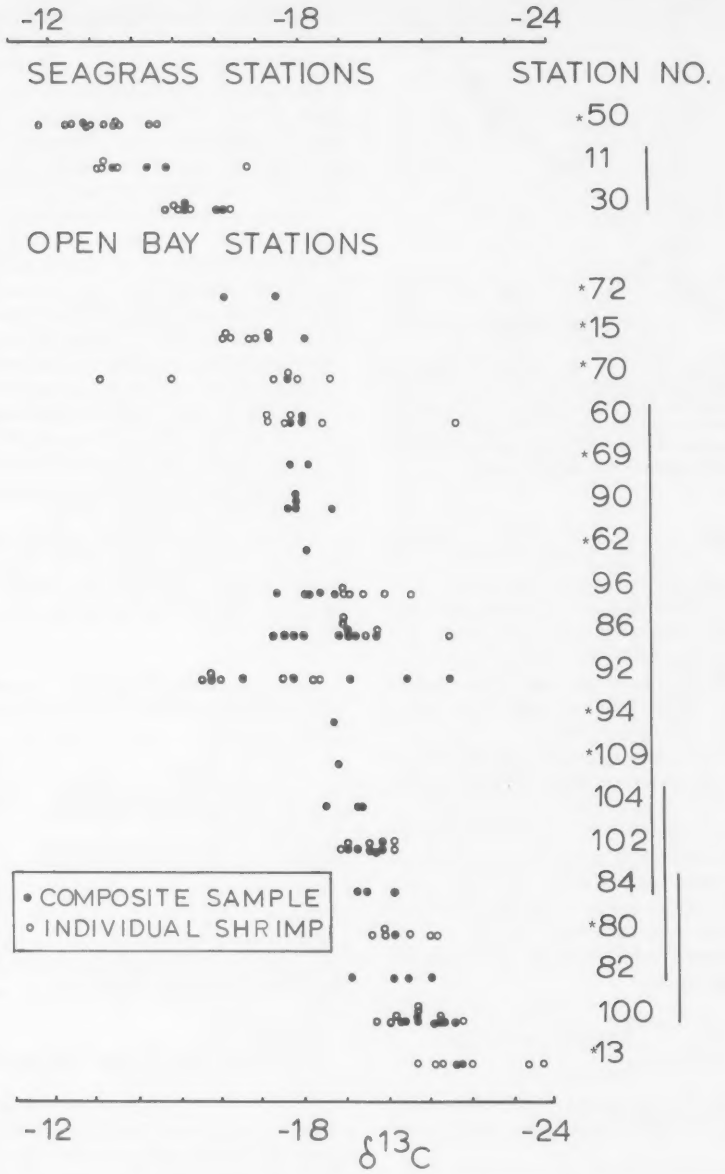

FIGURE 3.—Bay brown shrimp $\delta^{13}C$ by station, mid-April through mid-June 1978. Vertical lines (right margin) connect stations that, on the basis of their composite samples, were not significantly different ($P<0.01$, LSD multiple range test). Stations denoted by an asterisk had one or two composite samples and were not subjected to this analysis, although they are included for completeness. Stations 69 and 109 are composites of several stations in Aransas and Galveston Bay, respectively.

generally progressing throughout the spring sampling period. Both individual and composite bay brown shrimp samples were examined by station and station group (Figure 3) using graphic, linear, and multinomial regression analysis for correlations of shrimp length, weight, or date of collection with shrimp $\delta^{13}C$. These analyses were significant only rarely, <1 case in 10, so that no consistent $\delta^{13}C$ relationships with size or date were evident.

Offshore Samples

In addition to migratory brown shrimp, three other shrimp and stomatopod species were collected offshore at stations 200, 204, and 208. These species, *Trachypenaeus similis*, *Sicyonia dorsalis*, and *Squilla empusa*, are normally resident offshore and only occasionally enter estuaries (Hoese et al. 1968). Composite samples of these species fell within a narrow $\delta^{13}C$ range of −16.2 to −16.9‰ (Table 2). Forty-three individual rock shrimp, *Sicyonia dorsalis*, also collected at these stations showed a slightly larger $\delta^{13}C$ range of 1.9‰, −15.5 to −17.4 (Table 2). Mean $\delta^{13}C$ values of migratory brown shrimp were very similar to values of the resident species, although some $\delta^{13}C$ values of smaller brown shrimp differed significantly from mean values of the offshore species (Figure 4A, B). Several other samples of small brown shrimp collected offshore or during outgoing tides 24 May and 21 June 1978 at Aransas Pass Inlet also showed $\delta^{13}C$ values significantly different from the July offshore species (Figure 4A, B). These individual and composite analyses showed that small brown shrimp may enter the offshore regions with widely differing $\delta^{13}C$ values (−12.5 to −19.1‰, Figure 4). But as brown shrimp feed and grow offshore, their $\delta^{13}C$ values rapidly converge on the −16 to −17‰ $\delta^{13}C$ values characteristic of offshore, nonmigratory species.

TABLE 2.—$\delta^{13}C$ values of shrimp species caught at three offshore stations, July 1978. The standard deviation and the number of samples (N) are given after the means that contain more than one sample.

Item	Station 200	204	208
Composite samples:			
Offshore stomatopod			
Squilla empusa	−16.4	−16.2	−16.4
Offshore shrimp			
Trachypenaeus similis	−16.4	−16.6	−16.2
Sicyonia dorsalis	−16.4	−16.6	−16.9
Migratory brown shrimp	−16.6 ±.6(4)	−16.8 ±.2(4)	−16.2 ±.5(7)
Individual shrimp:			
Offshore *S. dorsalis*	−16.5 ±.4(12)	−16.2 ±.5(13)	−16.7 ±.4(16)
Migratory brown shrimp	−16.0 ±.7(12)	−16.2 ±1.0(12)	−15.9 ±1.2(16)

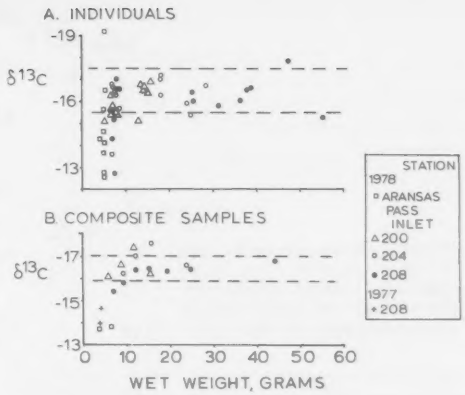

FIGURE 4.—Size dependence of brown shrimp $\delta^{13}C$ values at three offshore stations and from an outgoing tide at a major migratory pass opposite these stations. Dashed lines indicate 95% confidence limits beyond which single brown shrimp samples differ significantly from the −16.5‰ mean of resident offshore shrimp species listed in Table 2 (Sokal and Rohlf 1969).

Seasonality

To supplement the late spring bay collections, a longer term seasonal study was undertaken at sea grass station 30. In addition to the migratory pink and brown shrimp, three small, 20-50 mm TL, nonmigratory shrimp species were also collected: grass shrimp, *Palaeomontes* sp.; arrow shrimp, *Tozuema carolinense*; and snapping shrimp, *Alpheus heterochaelis*. Mean values of these two migratory and three nonmigratory species showed a sigmoidal variation from −15.6 in late April to −13.0 to −13.2 in late August through late October to −14.2 in early December (Figure 5). Regression analysis showed that mean $\delta^{13}C$ did not correlate significantly with either temperature or salinity. Collections offshore and at sea grass station 50 showed a similar pattern in shrimp $\delta^{13}C$ variation between early summer and late fall, although collections at these stations were not made regularly as at station 30. Late October offshore composite samples averaged 1.2‰ less negative than late July samples (N = 18 and 23, respectively); at sea grass station 50, late September composite samples averaged 2.2‰ less negative than late June samples (N = 4 and 2, respec-

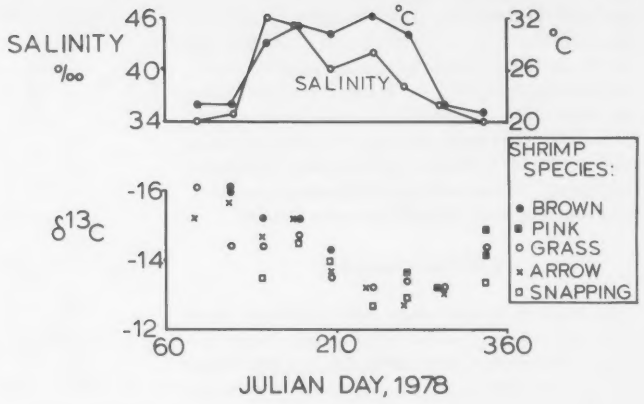

FIGURE 5.—Seasonal trends in shrimp $\delta^{13}C$ at bay sea grass station 30. All samples are composite samples; temperatures were taken between 0900 and 1200 h on each collection date.

tively). These seasonal differences between means were significant offshore ($P<0.01$, t-test) but not at sea grass station 50 ($P>0.05$, t-test).

DISCUSSION

To use $\delta^{13}C$ data to monitor shrimp migrations, isotopically distinct feeding grounds must be identified in which shrimp acquire significantly different, unique isotopic tags during feeding and growth. When the relationship between shrimp foods and shrimp tissue $\delta^{13}C$ is more precisely known, it should be possible to predict shrimp tissue $\delta^{13}C$ at any locality from the $\delta^{13}C$ value of locally available shrimp foods (Fry in prep.). This study relied on a more indirect method of identifying these isotopically distinct feeding grounds, i.e., monitoring the tissues of the mobile shrimp. In most cases, mean shrimp $\delta^{13}C$ values are probably a reliable index of local feeding conditions, as evidenced by the close $\delta^{13}C$ similarity of migratory brown shrimp and resident nonmigratory shrimp both offshore (Table 2) and in sea grass meadows (Figure 5).

Tests for significant differences among stations showed that sea grass stations were distinct from open bay stations which were in turn divided into two groups (Figure 3). The $\delta^{13}C$ distinction between sea grass and the more positive group of bay stations has been previously observed (Parker and Calder 1970; Fry et al. 1977; Fry and Parker 1979). These open bay stations occurred throughout the Texas bay system (Figure 3). The more negative open bay stations were found in areas which are more heavily influenced by terrestrial inputs such as sewage (stations 100 and 13) or river-borne debris (stations in Galveston and San Antonio Bays). Numerous sediment studies have documented that river-borne detritus derived from terrestrial sources averages -25 to $-30‰$ (e.g., Hunt 1970; Shultz and Calder 1976). Brown shrimp consumption of this detritus should result in the observed more negative shrimp $\delta^{13}C$ values.

Seasonality

The seasonal cycle observed in shrimp $\delta^{13}C$ is roughly correlated with the warmer growing season when the temperature increases and the species composition and abundance of food sources also change. These effects are difficult to separate with the present data. Marine plant species are sometimes enriched in ^{13}C when grown at higher temperatures (Sackett et al. 1965; Degens et al. 1968; Wong and Sackett 1978), although this effect does not appear to consistently apply to sea grasses (Thayer et al. 1978) nor to natural phytoplankton populations existing at temperatures typical of Texas bays (Sackett et al. 1974).

Seasonal changes in species composition and abundance occurring in sea grass meadows could also change the mean isotopic composition of shrimp foods; probably, the larger seasonal variations observed in sea grass meadows are due in part to the increasing dominance of sea grass carbon in food chains leading to shrimp. The lack of correlation between shrimp $\delta^{13}C$ values and temperature at a time when shrimp $\delta^{13}C$ values could change rapidly (mean weight increased 20-50 × over the spring sampling period) argues against a

direct temperature effect on the carbon metabolism of shrimp.

Offshore Migrations

As brown shrimp migrate offshore from the estuaries, they encounter a new feeding ground. During subsequent offshore growth, shrimp metabolize away the estuarine carbon present in their tissues, and dilute the remainder of this old carbon with new offshore carbon. Summer $\delta^{13}C$ values of nonmigratory offshore shrimp were quite constant around $-16.5‰$ and the offshore feeding grounds appeared to be isotopically uniform over the three stations sampled (Table 2). A model that incorporates these features and predicts the change of shrimp $\delta^{13}C$ during offshore growth is shown in Figure 6. This simple model is a first approximation in that only dilution of the old estuarine carbon during offshore growth is considered, while metabolic loss of this estuarine carbon is ignored. The $\delta^{13}C$ value of shrimp at any time after emigration can be calculated from the equation:

$$\delta^{13}C = \frac{\delta^{13}C_{old}(W_e) + (W_c - W_e)(\delta^{13}C_{new})}{W_c}$$

where W_e = initial weight at emigration,
W_c = weight at time of collection offshore,
$\delta^{13}C_{old}$ = $\delta^{13}C$ at emigration,
$\delta^{13}C_{new}$ = mean offshore shrimp $\delta^{13}C$.

The weights and $\delta^{13}C$ values at the time of offshore emigration shown in Figure 6 represent two individual brown shrimp collected in May at Aransas Pass Inlet (see Figure 4A). The 5 g wet weight is typical of most brown shrimp during the annual peak spring and early summer migrations (Copeland 1965; Trent 1966; Parker 1970; King 1971; pers. obs. 1978).

The model predicts that these migrating 5 g shrimp will rapidly become isotopically indistinguishable from resident shrimp during offshore growth (Figure 6). This prediction agrees well with the results shown in Figure 4 in which shrimp weighing >15 g are generally not significantly different than the –16.5 average of nonmigratory resident shrimp. Growth from 5 to 15 g should occur in about 1.1 and 2.9 mo for female and male brown shrimp, respectively (Parrack 1979), so that the effective offshore life of the estuarine tag is rather brief. Larger weights at emigration and increased differences between δ_{old} and δ_{new} result in a more gradual approach to the mean offshore value, while smaller weights, decreased $\delta_{old} - \delta_{new}$ differences, or metabolic loss of estuarine carbon during offshore growth would result in a shorter detectable life for this estuarine $\delta^{13}C$ tag.

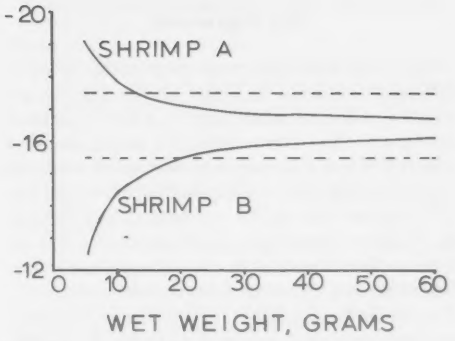

FIGURE 6.—Isotopic diet-change model for two shrimp migrating offshore from Texas estuaries. During offshore growth, these two shrimp gradually approach the characteristic $\delta^{13}C$ value of the offshore area, $-16.5‰$, according to the equation presented in the text. Dashed lines as in Figure 4 indicate $\delta^{13}C$ values at which the estuarine $\delta^{13}C$ tag is no longer distinguishable from normal offshore values.

The data presented in Figure 4 allow a preliminary assessment of the probable estuarine origins of most brown shrimp recruits to the offshore fishery. A trend among smaller shrimp towards $\delta^{13}C$ values more typical of sea grass meadows, rather than those typical of open bays, was evident at both Aransas Pass Inlet in May and June and offshore during late July (Figure 4). Shrimp from two other shallow-water habitats, salt marshes (Haines and Montague 1979), and blue-green algal mats (Fry, unpubl. data) also have isotopic compositions similar to shrimp from sea grass meadows. The $\delta^{13}C$ label thus distinguishes deeper water, open bays from shallow marsh, algal mat, or sea grass habitats. These initial results suggest that the shallow-water habitats are the more important feeding grounds for shrimp that enter the south Texas offshore commercial fishery. This conclusion is in good agreement with other studies that show that shrimp are exceptionally abundant in sea grass meadows (Loesch 1965; Young 1978) and that sea grass meadows are quite extensive in south Texas estuaries (Diener 1975).

Bay Migrations

The $\delta^{13}C$ data also trace migrations between different estuarine habitats. Brown shrimp are smaller and grow more rapidly in estuaries than offshore, further abbreviating the useful life of the initial $\delta^{13}C$ tag a shrimp possesses when entering a new feeding ground. Despite this, brown shrimp $\delta^{13}C$ values were highly variable at bay stations 60, 70, 86, and 92 (Figure 3). High variability may indicate that these stations lie on migration routes where shrimp converge from several isotopically distinct feeding grounds. In support of this idea, one may note that a high $\delta^{13}C$ range, 6.7‰, was observed among migrating individuals at Aransas Pass Inlet, and that offshore, small migrating brown shrimp caused a larger $\delta^{13}C$ range than that found in offshore resident species (Figure 4).

To identify which stations lie on migratory routes, one must distinguish the normal variability expected from local feeding conditions from a higher variability due to migration. Local variation is probably 2.2‰ or less and 3‰ or less for composite and individual samples, respectively. These estimates are based on the $\delta^{13}C$ ranges observed at frequently sampled bay stations, i.e., stations 90, 100, and 102 for composite samples and station 50 for individual samples (Figure 3). Further study will undoubtedly refine these estimates, or, alternatively, future studies may use large differences between shrimp tissue $\delta^{13}C$ and local food $\delta^{13}C$ as a criterion to identify locations where migratory activity occurs. These techniques should allow the delineation of underwater migratory routes whose existence has been suggested by Parker (1970).

CONCLUSION

This paper proposes to trace shrimp movements by matching the $\delta^{13}C$ values of migrating shrimp with the $\delta^{13}C$ values of shrimp living in habitats such as sea grass meadows and planktonic bays where available shrimp foods, and hence the shrimp themselves, differ substantially in their $\delta^{13}C$ values. There are several limitations to this method, as well as some advantages. The utility of the method is limited by the number of habitats that $\delta^{13}C$ analysis can differentiate. Future analyses of other stable isotopes such as hydrogen/deuterium may allow additional distinctions between habitats such as marshes and sea grass meadows. The rapid growth rate of shrimp imposes a second limitation. The maximum amount of information about migratory movement is gained by sampling slower growing animals soon after they begin their migrations. For shrimp, sampling males offshore or in migratory passes during the times of peak migrations will give clearest results. Seasonal changes in shrimp $\delta^{13}C$ occur, but are gradual and can be avoided by sampling during the 1-3 mo peak migration period.

This method should be equally applicable to other migratory animals, both terrestrial and aquatic. Fish movements may be easier to analyze than those of shrimp because of the age-specific $\delta^{13}C$ historical records that fish lay down in their scales. Such analyses could yield information not only about which areas an animal had fed in, but also at what stage in the life cycle and with what frequency these feeding episodes occurred. The initial data presented for the south Texas coast show that shallow water habitats such as sea grass meadows are important suppliers of shrimp to commercial fisheries. Direct extensions of these investigations should yield quantitative information on which estuarine habitats supply the bulk of shrimp and fish caught in commercial fisheries.

ACKNOWLEDGMENTS

Gill Gilmore and the staff of the Coastal Fisheries Division, Texas Parks and Wildlife Department, kindly made their spring shrimp collections available for analysis. P. L. Parker and R. S. Scalan provided support and technical assistance. Chris L. Kitting, Joan Holt, and two anonymous reviewers made useful criticisms of early drafts of this manuscript. This work was supported by NSF grant OCE 77-27009.

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NOTES

ANNUAL REPRODUCTION, DEPENDENCY PERIOD, AND APPARENT GESTATION PERIOD IN TWO CALIFORNIAN SEA OTTERS, *ENHYDRA LUTRIS*

There are various estimates of the frequency of pupping, dependency period and gestation period for the sea otter, *Enhydra lutris*. Based upon an evaluation of female urogenital tracts taken at various times of the year and comparing observed population growth rates with theoretical growth rates, Kenyon (1969) and Schneider[1] concluded that female sea otters probably reproduced every 2 yr. Sinha et al. (1966) demonstrated that delayed implantation of the blastocyst probably occurred in sea otters. Kenyon (1969) suggested 12-13 mo total gestation period (7-8 mo unimplanted and 4.5-5.5 mo implanted) and 11-12 mo for rearing the pup, and a few months rest between weaning and the next estrus. This cycle could be shortened if the female prematurely lost a pup (Schneider footnote 1). Schneider[2] assumed the reproductive cycle included a 7.5 mo gestation period; Barabash-Nikiforov (1935) estimated an 8-9 mo gestation period; he later stated that sea otters breed once a year (Barabash-Nikiforov 1969). Lensink (1962) believed that females bred every year, at least when food was not limiting, and recent evidence presented by Johnson and Jameson[3] indicates annual reproduction in at least some Prince William Sound sea otters. Vandevere (1972) suggested that pup dependency period was less than a year, based on an annual February peak in pupping in California.

This note describes observations of two tagged female sea otters in California, one seen with a different pup for 6 consecutive yr and the other seen with four different pups in about 5 yr. We also report estimates on the apparent gestation period and pup dependency period for these two sea otters.

The first sea otter was a female [No. 34; marked with aluminum tags (Loughlin 1977)] weighing 22 kg when captured on 7 March 1976 near Monterey, Calif. It was noted at the time that this female had protruding nipples, a distended abdomen, an enlarged pelvic area, indicating that she may have been pregnant. She was subsequently seen on 13 March 1976 with a newborn pup. The female-pup pair was last sighted on 2 April 1976, although the female was sighted often in May 1976 without a pup. The pup was apparently lost after only 2 mo and probably died. On 9 May 1977, female No. 34 was seen with a second pup estimated to be 1-3 mo old near San Simeon, Calif. (approximately 140 km south of Monterey). The last sighting of this pup was on 10 August 1977 at which time it was assumed to be 4-6 mo old. [The pups were not marked, except for No. 34's third pup, and since sea otters are not known to adopt strange pups, we assumed that the pups observed were the same during any 1 yr. Estimates of age for pups were based upon a subjective appraisal of physical appearance and behavior (Lensink 1962; Kenyon 1969; Sandegren et al. 1973). The reader is cautioned that our estimates of gestation period are based upon this subjective appraisal.] A third pup, a 3.6 kg female probably not over 1.5 mo old, was captured along with No. 34 on 2 March 1978 back near Monterey. This pup was marked with a small tag in one ear and was sighted only once about a week later. It is presumed to have died. Number 34 was observed on 9 January 1979 with a fourth pup. Both were resighted on many occasions through 13 September 1979 when this pup was assumed to be slightly over 8 mo of age. This same female was seen with a fifth newborn pup on 27 March 1980. This mother-pup pair was seen on at least two subsequent occasions, the last being 8 April 1980, but by 5 May 1980 she again was without a pup and it presumably died. Number 34 was seen with her sixth pup, judged to be 1 mo old, on 9 March 1981 and it was still with the female at the time of writing (Table 1). (Identification of No. 34 is now difficult since she lost her right flipper tag and the left is loose.)

The second female sea otter (No. 41) weighed 25 kg when captured and marked on 15 August 1976 near Monterey. She was observed on 8 January 1977 with a newborn pup and both were subsequently resighted on many occasions. Eight months later, on 8 September 1977, she had a red swollen nose which is indicative of recent copulatory behavior (Kenyon 1969) and was without her

[1]Schneider, K. B. 1972. Reproduction in the female sea otter. Alaska Department of Fish and Game, Sea Otter Rep. I, 36 p.

[2]Schneider, K. B. 1973. Reproduction in the female sea otter. Alaska Department of Fish and Game, Sea Otter Rep. II, 13 p.

[3]Johnson, A. M., and R. Jameson. 1979. Evidence of annual reproduction among sea otters. (Abstr.) Third Biennial Conference on the Biology of Marine Mammals, Oct. 7-11, Seattle, Wash., p. 31.

TABLE 1.—Observation data on sea otter No. 34 and her six pups.

Pup	Date pup first seen	Approximate age of pup when first seen	Date pup last seen	First date female seen without pup	Approximate dependency period	Apparent gestation period
First	13 Mar. 1976	Newborn	2 Apr. 1976	10 May 1976	Presumed dead	No estimate
Second	9 May 1977	1-3 mo	10 Aug. 1977	12 Aug. 1977	4-6 mo	About 5 mo
Third	2 Mar. 1978	About 1.5 mo	7 Mar. 1978	15 Mar. 1978	Presumed dead	No estimate
Fourth	9 Jan. 1979	Newborn	13 Sept. 1979	22 Sept. 1979	8.5 mo	6 mo
Fifth	27 Mar. 1980	Newborn	8 Apr. 1980	5 May 1980	Presumed dead	No estimate
Sixth	9 Mar. 1981	About 1 mo	Still with female at time of writing			

TABLE 2.—Observation data on sea otter No. 41 and her four pups.

Pup	Date pup first seen	Approximate age of pup when first seen	Date pup last seen	First date female seen without pup	Approximate dependency period	Apparent gestation period
First	8 Jan. 1977	Newborn	27 Aug. 1977	8 Sept. 1977	8 mo	4 mo
Second	28 Feb. 1978	About 1.5 mo	7 Sept. 1978	27 Sept. 1978	8 mo	4 mo
Third	13 Mar. 1979	About 1.5 mo	5 May 1979	10 July 1979	3.5-5.5 mo	No estimate
Fourth	31 Dec. 1980	About 1.5 mo	Still with female at time of writing			

pup (Table 2). She was seen with a second pup judged to be about 1.5 mo old on 28 February 1978. This mother-pup pair was seen on numerous occasions through 7 September 1978. Apparently the mother and pup separated after about 8 mo. Number 41 was observed with a third pup, also judged to be approximately 1.5 mo old, on 13 March 1979. This pair was observed often through 5 May 1979. Neither was seen again until 10 July 1979 when No. 41 was seen, red nosed, with a male but without her pup. The third pup, therefore, probably was 3.5-5.5 mo old when separated from its mother. Number 41 was seen with a fourth pup, judged to be 1.5 mo old, on 31 December 1980, and was still with the female at the time of writing.

Since it is not possible to determine with certainty when conception or blastocyst implantation occurred, we can only speculate on the gestation period for the pups of No. 34 and 41. On 10 August 1977, No. 34 was seen with a second pup and on 12 and 13 August 1977 she was seen without her second pup and with a male escort. Photographs of her head region taken on 13 August 1977 showed nose damage indicating recent copulation. She was subsequently recaptured on 2 March 1978 with a third pup that weighed 3.6 kg. Assuming the pup was 1.5 mo old at capture and that conception occurred in mid-August 1977, the gestation period was about 5 mo. Number 34 and a fourth pup were last seen together on 13 September 1979. She was seen without a pup and with a male companion on 22 September 1979 and by 24 September 1979 her nose again exhibited evidence of recent copulation. We monitored No. 34 closely for the next several months. She was last seen without a pup on 14 March 1980; then with a fifth pup on 27 March 1980. If conception took place on 22-24 September 1979, gestation was close to 6 mo.

Number 41 was separated from a pup in early September 1977, coincident with the appearance of a male companion. She had a swollen nose on 8 September 1977 and on 28 February 1978 was seen with an estimated 1.5-mo-old pup. Assuming conception occurred in early September, the gestation period was a little over 4 mo. Her second pup was "weaned" in early September 1978. A third pup, judged to be about 1.5 mo old when first observed on 13 March 1979, was also born just over 4 mo after separation of the second.

Our observations indicate that at the time of separation (weaning) three of the eight separated pups were large enough at 8-8.5 mo of age to have a good chance of survival. Two pups between about 3.5 and 6 mo, although rather small, may have survived. Some independent animals have been documented in the 9-12 kg range (Loughlin 1977; Wild and Ames[4]). The remaining three almost certainly died.

Estimates of the gestation period for captive sea otters, presumably based upon more definitive data, range from 5.5 to 8 mo (Brosseau et al. 1975; Antrim and Cornell 1980; Antrim[5]). Our esti-

[4]Wild, P. W., and J. A. Ames. 1974. A report on the sea otter, *Enhydra lutris* L., in California. Calif. Dep. Fish Game, Mar. Resour. Tech. Rep. 20, 93 p.

[5]J. Antrim, Curator of marine mammals, Sea World, Inc., 1720 South Shores Road, San Diego, CA 92109, pers. commun. June 1980.

mates of 4-6 mo gestation periods, which assume that copulation and conception do not occur until after weaning, seem reasonable if the blastocyst is implanted soon after conception, partially skipping or entirely skipping the delay period. Our field data and that from captive studies indicate that the gestation period in sea otters may be variable and depend on an external stimulus or the general well being of the female.

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MASS MORTALITY OF FEMALE DUNGENESS CRAB, *CANCER MAGISTER*, ON THE SOUTHERN WASHINGTON COAST

Studies of growth and age of Dungeness crab, *Cancer magister*, populations from California to British Columbia have amply elucidated developmental rates for this species (Cleaver 1949; Waldron 1958; Butler 1961; Poole 1967), but no information is contained in such reports on mortality and its causes, apart from reference to known predators and cannibalism. Natural mortality for highly mobile crustaceans is difficult to investigate because animals simply do not expire in easily observed locations or are quickly removed by scavengers once dead. Consequently, there has been no documentation of extensive crustacean mortality by causes such as disease or pollution on the Pacific coast of the United States, and therefore loss from a population throughout its life cycle due to a generalized predator category (including fishing and cannibalism for *C. magister*, Botsford and Wickham 1978) remains the traditional mortality component of the literature on many crustaceans including Dungeness crabs.

On 18 April 1979 large numbers of dead Dungeness crabs on the beach at Grayland, Wash. (Figure 1), were reported to the Westport Field Office of the Washington Department of Fisheries (WDF). Inspection of the beach between Westport and the northern end of Willapa Bay confirmed that many Dungeness crabs had been washed ashore and, contrary to our initial supposition, were not exuvia which are often mistaken for dead crabs by the public. Preceding this instance, we had reports of dead crabs in the pots of commercial fishermen in Willapa Bay in February 1979, and these findings were verified by WDF personnel.

In response to the report of 18 April, five locales on the beach from Grays Harbor to Willapa Bay (Figure 1, Table 1) were quantitatively examined for dead crabs and the shoreline between these points was inspected from a car. All crabs along the five transects were counted and sexed, if possible, and 42 Dungeness crabs at transect 3 were measured to the nearest millimeter across the carapace inside the tenth anterolateral spines.

Results

Dead crabs found on the beach between Grays Harbor and Willapa Bay were confined to the line of previous high tide in a swath about 8-10 m wide.

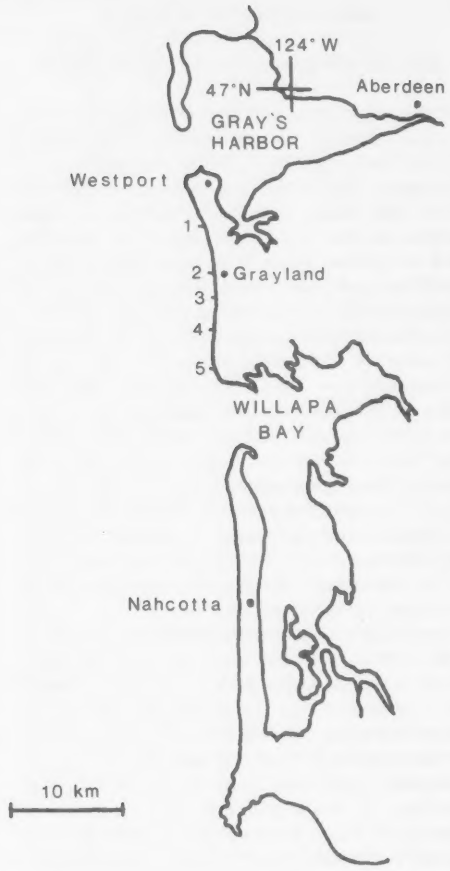

FIGURE 1.—Southern Washington coast and locations of numbered transects.

Nearly all animals examined contained musculature in the appendages and thoracic region and relatively few exuvia were found (Table 1). Because of decomposition and some bleaching of shells, animals were judged to have been on the beach 1-3 d and a relatively high percentage had been damaged by scavenging birds, thereby precluding identification of sex in those instances. Still, all Dungeness crabs sexed were females which, of the 42 measured, averaged 147 mm carapace width (range 110-162 mm).

TABLE 2.—Estimated number of dead Dungeness crabs, Grayland to North Cove, Wash., 18 April 1979.

Area	Crabs/m[1]	Distance between transects (m)	Estimated total no. dead crabs between transects
Grayland to county line (transects 2 to 3)	1.09	1,800	1,962
County line to Midway (transects 3 to 4)	1.15	2,700	3,105
Midway to North Cove (transects 4 to 5)	0.41	3,400	1,394
Total			6,461

[1]Average of two successive transects.

Substantial numbers of dead crabs were found with densities of up to 1.64 crabs/m of shoreline (in the 8-10 m band of upper high tide) computed at transect 3 (Table 1). Generally, the numbers of dead crabs observed between transects seemed consistent with the densities recorded along transects. Estimation of the total number of dead crabs on the beach between Grayland and North Cove (7.9 km) was 6,461 animals (Table 2).

Discussion

Mass mortality of *C. magister* has not, to our knowledge, been previously reported for any locale within this species range from central California to Alaska. At the time of the incidence we describe for southern Washington, there were no similar reports of mortality along Oregon beaches according to Dale Snow.[1] Furthermore, he had never verified an occurrence of extensive crab mortality in that state during 17 yr of fisheries research.

Does our report then, describe an isolated or rare phenomenon of this species or does an event such as mass mortality go undetected, observed but not interpreted for what it is? Along the Wash-

[1]Dale Snow, Oregon State Department of Fish and Wildlife, Newport, Oreg., pers. commun. April 1979.

TABLE 1.—Dead Dungeness crabs along measured beach transects in southern Washington (shown in Figure 1).

Area and transect no. on map	Dead crabs				Exuvia	Transect length (m)	Crabs/m	Cumulative distance (km)
	M	F	Unknown	Total				
Twin Harbors - 1	0	0	0	0	3	152	0.00	0.0
Grayland - 2	0	26	5	31	1	61	0.54	4.3
County Line - 3	0	81	21	101	2	61	1.64	6.1
Midway - 4	0	14	27	41	5	61	0.66	8.7
North Cove - 5	0	4	5	9	0	61	0.16	12.2

ington coast, *C. magister* females generally molt and breed in April through June (Cleaver 1949), and local residents are accustomed to the presence of numerous cast shells on the beach at that time. Since it occurred in the spring, the mortality, prior to our investigation, was probably mistaken for normal molting by many people including patrolmen of the local state parks. It is possible, therefore, that similar occurrences have gone unreported in the past due to such confusion; careful examination of the shells is required to detect tissues and distinguish dead animals from exuvia.

Since the original drafting of this report, two additional mortalities have come to our attention. On 29 November 1979, Walt Cooke[2] observed a large number of dead female Dungeness crabs on the beach from Ocean Park to Long Beach, Wash. (15.6 km). He estimated their number to be 955-1,910, of which only 2.5% were exuviae, and 93% of the remainder were females averaging 146 mm (n = 58) carapace width. On 30 January 1980, Darrell Demory[3] estimated a mortality of 68 crabs/km from the Umpqua River mouth north to Tahkenitch Creek, Oreg., (13.9 km) for an estimated total of 947, of which approximately 95% were females. Conditions of both these occurrences were similar to the April mortality; each consisted almost entirely of large female crabs confined to the high tide line, and occasionally in patches.

It is noteworthy that several instances of dead Dungeness crabs in commercial pots from Willapa Bay prompted investigations by one of the authors, David Armstrong, and personnel from WDF and the National Marine Fisheries Service in February and March 1979 (Tufts[4]). Moribund and dead crabs (male and female) were found in pots checked every 24 h, and some were recovered from shallow intertidal areas. This indicates that animals attracted to bait were healthy enough to enter pots, and then died within a short time thereafter. These observations were made following a severe cold spell during which the air temperature was below freezing for 2 wk, and parts of Willapa Bay had frozen over suggesting temperature stress associated with the mortalities.

Causes of the mortality of April 1979 are only speculative, since crabs could not be examined histologically. Immediately after verifying the report, we questioned WDF personnel to learn if nearshore groundfisheries might account for extensive crab mortality by trawling activity, and learned that no trawlers were known to be operating just prior to 18 April offshore from the transect locations. We surmise that death was due to disease, and the specificity shown for large, older females indicates a causative agent linked perhaps to a decline in vigor with old age. Female *C. magister* reach sexual maturity at about 100 mm carapace width in their second year and relatively few animals exceed 145-150 mm (Butler 1961; Poole 1967). The average carapace width of 147 mm for dead crabs at transect 3 shows a preponderance of older females were affected, perhaps because they were more susceptible to possible lethal stresses than younger animals.

Tissue samples dissected from moribund animals in Willapa Bay in March 1979 were studied for histopathological anomalies, and preliminary results indicate a systemic bacterial infection as a possible causative agent according to Sparks.[5] Lethal diseases among wild populations of *C. magister* are unknown but mortalities of laboratory-held animals have been attributed to such pathogens as fungus and ciliates (Armstrong et al. 1976; Armstrong and Sparks[6]). It seems likely that bacteria or various pathogenic protozoans may take a toll in wild populations, particularly in a segment of the population weakened or predisposed by contributing factors such as old age.

Demory (footnote 3) concluded that the mortality observed in January 1980 on the Oregon beaches may have been the result of stress on crabs trapped in pots that were "sanded in" during a period of adverse weather immediately preceding the observation, when fishermen could not pull these pots for several days. No diseases or parasites were found in specimens obtained from this mortality.

Although examples of mass mortality in crustacean populations are rare, the presence of numerous dead *C. magister* along a beach is reminiscent of the "Gray Crab Disease" affecting *Callinectes sapidus* on the east coast of the United States. Lethal infections attributed to the amoeba

[2]Walt Cook, Washington Department of Fisheries, P.O. Box 158, Ocean Park, WA 98640, pers. commun. 2 June 1980.
[3]Darrell Demory, Oregon State Department of Fish and Wildlife, Newport, Oreg., pers. commun. 5 February 1980.
[4]Dennis Tufts, Washington Department of Fisheries, P.O. Box 158, Ocean Park, WA 98640, pers. commun. 11 July 1980.
[5]Albert Sparks, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, Wash., pers. commun. March 1979.
[6]D. Armstrong and A. Sparks, College of Fisheries, University of Washington, Seattle, WA 98195, unpubl. data on blood ciliates.

Paramoeba perniciosa have been found from Maryland to Georgia (Sprague et al. 1969; Mahood et al. 1970), and strong correlations were established between mass mortalities of blue crabs, high incidences of infection, and declines in commercial fishery landings (Mahood et al. 1970). Percentages of blue crabs infected with the disease range from 20 to 35% of captive animals in holding boxes (Sprague and Beckett 1966; Sawyer 1969) and from 7 to 17% in wild populations during the summer (Sawyer 1969; Sawyer et al. 1970; Newman and Ward 1973). As noted by Newman and Ward, epizootics attributed to this disease can be of short duration, killing significant numbers of animals and leaving no indication of the severity even to investigators purposefully seeking clues on occurrence and extent of infection.

The importance of these observations is, in part, as a reminder that significant loss from a population can result from factors other than predation. The nature of other mortality factors (be they disease, physical-chemical, or pollution) and the magnitude of their effects are largely unknown, particularly for highly mobile crustaceans. Still, the presence of over 6,400 dead adult female crabs along a segment of coastline in conjunction with the other two reports of mass mortality noted, indicates *C. magister* is susceptible to conditions and events that may occur on a seasonal basis. It is reasonable to assume that the crabs observed dead at the high watermark were only a fraction of the numbers affected offshore and, if so, then the magnitude of the mortality in this instance was certainly greater than that observed.

Whatever the cause of the mortality to *C. magister* in this case, and whether such an event is a common seasonal occurrence or a rare catastrophe, a partial loss of this reproductively significant age-group could have important consequences for the commercial fisheries.

Acknowledgments

We express our appreciation to Walt Cooke and Dennis Tufts of the WDF, to Albert Sparks of the National Marine Fisheries Service, and to Darrell Demory of the Oregon Department of Fish and Wildlife for sharing their observations with us.

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FISHES NEW TO THE EASTERN BERING SEA

A joint Japan-United States groundfish survey was conducted during the summer of 1979 on the continental shelf and slope in the eastern Bering Sea. Of the more than 100 species of fishes taken during the survey, 1 has not been previously reported from the Bering Sea—*Kali indica* Lloyd 1909 (Chiasmodontidae)—and 3 others have been recorded, but no specific localities in the eastern portion have been attributed as capture sites: *Percis japonicus* (Pallas 1772) (Agonidae); *Laemonema longipes* Schmidt 1938 (Moridae); and *Macropinna microstoma* Chapman 1939 (Opisthoproctidae). In this paper we document the capture of the four species from the eastern Bering Sea.

Collection Information (Table 1)

Specimens of the four species were captured with a 53.4 m (headrope length) commercial bottom trawl fished by a 350-ton land-based trawler, the *Yakushi Maru No. 21*, chartered by the Fisheries Agency of Japan. As no closing devices were used, capture depths are unknown. Presumably, the specimens of *Kali*, *Laemonema*, and *Macropinna* species were captured in midwater as the trawl was lowered or raised, for the species have been collected previously almost exclusively by midwater trawls. Specimens are deposited in the Laboratory of Marine Zoology, Hokkaido University, Hakodate (HUMZ), and the U.S. National Museum of Natural History, Washington, D.C. (USNM). Other specimens of *Percis japonicus* and *Laemonema longipes* were examined from the collections of the Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, Kodiak, Alaska, and the College of Fisheries, University of Washington, Seattle, Wash. (UW), respectively.

TABLE 1.—Collection data for the eastern Bering Sea fish specimens (summer 1979).

Station no.	Date (GMT)	Position (middle of tow)	Bottom depth (m)	Water temp. (°C)	
				Surface	Bottom
22	27 June	59°47.9′ N 178°47.3′ W	930	7.5	3.0
28	27 June	59°53.0′ N 178°54.3′ W	580	7.2	3.7
43	27 June	59°28.6′ N 178°12.5′ W	280	6.5	—
124	23 June	58°22.1′ N 175°01.8′ W	740	6.3	—
225	7 July	57°00.6′ N 170°16.2′ W	510-440	8.1	3.2
251	18 June	56°00.9′ N 169°16.5′ W	610	6.8	—

Kali indica Lloyd 1909
Figure 1 (upper)

One specimen, HUMZ 81941, taken at station 124. This bathypelagic chiasmodontid is widely distributed in tropical seas and has been taken in the temperate South Atlantic and North Pacific as well (Johnson 1969; Johnson and Cohen 1974). Hubbs et al. (1979) have recently reported it from off California based on two specimens (lat. 32°37.7′ N, just north of the United States-Mexican border; and about lat. 33° N, long. 119°20′ W; locality information from L. J. Dempster[1]). The Bering Sea specimen is the most northern record of the species, the first from boreal waters, and an addition to the fish fauna of Alaska.

Counts: D. XIII+24; A. I,25; P. 11; V. I,5; branchiostegal rays 6. Teeth: in lower jaw 5 (outer row) and 3 (inner row); in upper jaw 6 (outer) and 3 (inner); on palatine 4. Measurements in millimeters: standard length 175.3; predorsal 48.5; preanal 95.8; greatest body depth 30.1; least depth caudal peduncle 7.6; length caudal peduncle 20.6; pectoral fin length 30.9; head length 41.6; snout 14.5; eye diameter 6.2; postorbital length of head 22.8; width bony interorbital 11.6; length upper jaw 34.2; length lower jaw 37.2; largest teeth on upper jaw 8.9.

Percis japonicus (Pallas 1772)
Figure 1 (lower)

One specimen, HUMZ 84945, taken at station 43; another deposited in the Northwest and Alaska Fisheries Center Kodiak Laboratory, NMFS, from lat. 57°16.3′ N, long. 172°56.5′ W (RV *Oregon* cruise 794, haul 90, 23 July 1979). Other specimens have been taken from the eastern Bering Sea northwest of Unalaska.[2] This agonid is common in Japanese waters and is also known from the Okhotsk Sea and the Asiatic coast of the

[1]Lillian J. Dempster, Associate Curator, Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, pers. commun. January 1980.

[2]Doyne Kessler, Fishery Biologist, Northwest and Alaska Fisheries Center Kodiak Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615, in litt., 5 August 1980, and James Long, student, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, pers. commun. 9 September 1980.

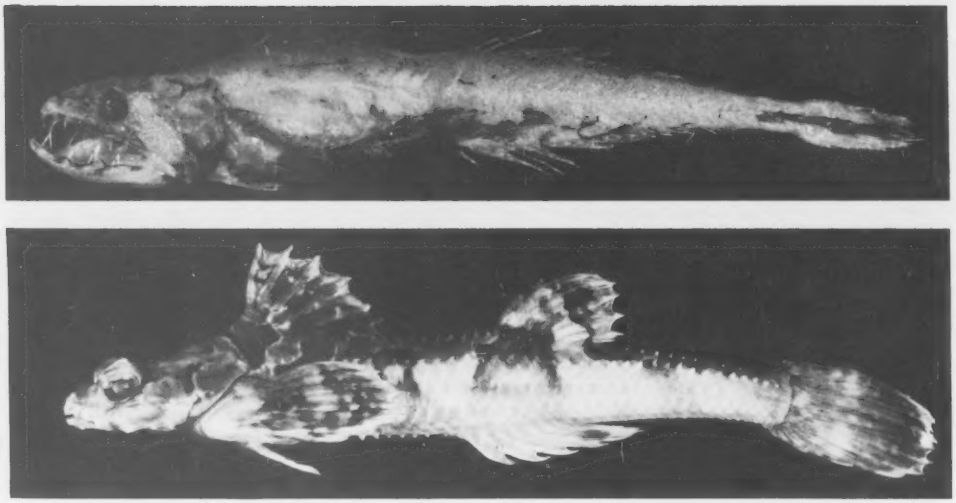

FIGURE 1.—Specimens of *Kali indica*, HUMZ 81941 (top) and *Percis japonicus*, HUMZ 84945 (bottom) taken in the eastern Bering Sea.

Bering Sea (Jordan and Gilbert 1899; Andriashev 1937; Schmidt 1950). Schultz (1967) quoted a letter from Teodor Nalbant which mentions a capture in the south-central Bering Sea, but without an exact locality. The present specimens are the first certain records of the species from the eastern Bering Sea and an addition to the fauna of North America.

Counts (HUMZ 84945 first): D. VI+7, VI+7; A. 8, 8; P. 12, 12; V. I,2, I,2; lateral line plates 30, 37; vertebrae (excluding ural centrum) 40, —. Measurements in millimeters (HUMZ 84945 first): standard length 241, 215; predorsal 66.0, 60.3; preanal 131.0, 122.6; preventral 61.2, 61.8; greatest body depth 40.5, 35.9; least depth caudal peduncle 16.8, 17.5; pectoral fin length 56.0, 50.2; ventral fin length 31.5, 29.2; first dorsal fin base 48.2, 39.8; second dorsal fin base 33.1, 32.2; anal fin base 69.1, 40.3; head length 60.8, 55.4; snout length 15.4, 15.7; eye diameter 12.2, 8.9; interorbital width 16.2, 16.1; upper jaw length 15.3, 13.0.

Laemonema longipes Schmidt 1938

Two specimens, HUMZ 82892 and USNM 220877, were collected at station 251; a third example, UW 20772, eastern Bering Sea, summer 1978, was also examined. This elongate morid is locally abundant in the western North Pacific, ranging from off Owase, Mie Prefecture (specimens in the collections of the University of Kyoto, Maizuru), to the Okhotsk and Bering Seas. Large trawl catches from Suruga Bay have been noted by Matsubara (1955), and >1,000 individuals were found in the stomach of a whale in the Kurile-Kamchatka Trench (Rass 1954). Although Fedorov (1973) listed the species from the Bering Sea, apparently no specimens or precise localities documenting the record have been published. These specimens are new additions to the fauna of North America.

Counts (HUMZ 82892 first, followed by USNM 220877 and UW 20772): D. 6+52, 6+52, 6+50; A. 49, 50, 50; P. 17, 17, 18; V. 2, 2, 2; caudal rays 23, 25, 22; gill rakers 7+18, 8+21, 8+22; branchiostegal rays 7, 7, —; vertebrae (not including ural centrum) 52, 53, 50. Measurements in millimeters: standard length 178, 219, 205; predorsal 46.9, 57.1, 54.7; preanal 68.7, 78.1, 77.1; preventral 34.8, 40.1, 38.1; greatest body depth 39.9, 34.0, —; pectoral fin length 39.8, 46.2, 43.9; ventral fin length 71.0, 78.4, 64.5; head length 42.9, 49.6, 46.3; snout 13.0, 15.8, 14.2; eye diameter 7.4, 9.3, 8.6; width interorbital 9.4, 15.2, 12.8; length upper jaw 20.0, 23.3, 22.1.

Macropinna microstoma Chapman 1939

Three specimens were taken: HUMZ 81966 (stn. 22), HUMZ 81975 (stn. 28), and USNM 220876

(stn. 225). This bizarre, tube-eyed opisthoproctid fish is a characteristic member of the mesopelagic fauna in the temperate eastern North Pacific, where it has been caught between the Gulf of Alaska and northern Baja California (Berry and Perkins 1966; Quast and Hall 1972). It also has been taken in the southeastern Pacific west of the Juan Fernández Islands (Craddock and Mead 1970). Although no localities have been presented, western Pacific captures are mentioned from the Kurile-Kamchatka Trench (as Macropinnidae; Rass 1955) and listed from the northwestern Pacific (Parin 1961). Fedorov (1973) listed the species from the Bering Sea without documentation. The three specimens reported upon here are the first verified records of the species from the Bering Sea.

Counts and measurements of HUMZ 81966 (eyes, distal portion of ventral fin, and skin lost), HUMZ 81975 (eyes, dorsal fin, and skin lost), USNM 220876 (eyes lost). Counts: D. 11, —, 12; A. 14, 14, 14; P. 17, 17, 17; V. 10, 10, 10; branchiostegals 3, 3, 3. Measurements in millimeters: standard length 96.4, 112.8, 56.7; predorsal 68.6, —, 42.7; preanal 76.7, 82.5, 41.9; preventral 53.3, 61.7, 33.1; vent to anal origin 22.1, 18.0, 6.1; greatest body depth 36.6, 36.8, 20.3; least depth caudal peduncle 13.2, 14.3, 7.3; pectoral fin length 21.6, 17.8, 16.5; ventral fin length —, 48.9, 28.0; dorsal fin base 15.8, —, 8.8; anal fin base 14.3, 18.4, 9.6; head length 38.0, 47.8, 26.6.

Acknowledgments

We thank Alex E. Peden, British Columbia Provincial Museum, and Doyne Kessler, Northwest and Alaska Fisheries Center Kodiak Laboratory, NMFS, for the loan of specimens. Kunio Amaoka and Tsutomu Kanayama, Hokkaido University, gave useful advice.

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SCHOOLING OF THE SCALLOPED HAMMERHEAD SHARK, *SPHYRNA LEWINI*, IN THE GULF OF CALIFORNIA

Groups of sharks have been witnessed occasionally by airborne or shipboard observers (Bass et al. 1975; Clark 1963; Springer 1967; Kenney 1968). Such remote observations, augmented with inferences from fishery records (Ford 1921; Olsen 1954; Jensen 1965), have provided fragmentary descriptions of these groups and speculations on their function. We have studied polarized schools of the scalloped hammerhead shark, *Sphyrna lewini*, by free diving among them at several offshore sites in the Gulf of California. Here we report preliminary observations on the sizes, depths, movements, and compositional dynamics of these schools, and the sizes, sexes, and behavior of the school members. Based upon these observations, we discuss the possible function of such schools.

Previous sightings by others indicated that schools of *S. lewini* might be encountered during the summer at three locations near La Paz, Baja California Sur, Mexico: Las Arenitas Rocks (Isla Cerralvo), El Bajo Espiritu Santo, and Isla Las Animas (Figure 1). These locations were visited between 26 July and 6 August 1979 aboard either our 7 m fiber glass skiff or the 23 m ferrocement research vessel, the *Juan de Dios Batiz*. At these locations and others, four search techniques were employed: 1) Free diving and surface swimming; 2) scuba; 3) baiting with ground Pacific mackerel, *Scomber japonicus*; and 4) playback of pulsed, low-frequency sounds (for description, see Myrberg 1978). Scalloped hammerheads were most easily discovered and approached by free diving, and data were recorded on small plastic slates. Relatively few scalloped hammerheads were observed by divers with scuba, even in areas where this species was abundant. This was probably due to their avoidance of the divers' sounds and visually conspicuous bubbles. Only three scalloped hammerheads were attracted in 11.5 h of baiting and none during 40 min of sound playback, indicating a lack of interest in these feeding stimuli.

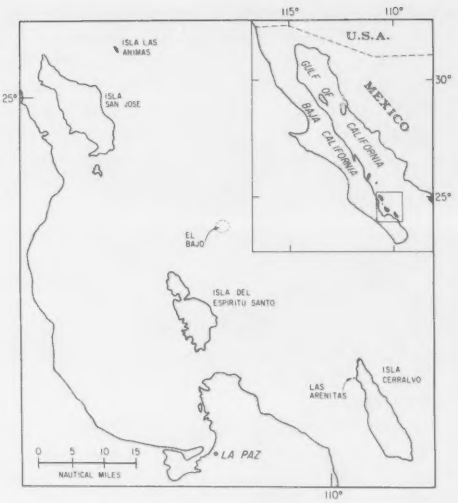

FIGURE 1.—The La Paz study area in the Gulf of California. Grouped scalloped hammerhead sharks were encountered at three sites: 1) Las Arenitas, a cluster of rocks 100 m from Isla Cerralvo; 2) El Bajo Espiritu Santo, a seamount rising to within 14 m of the sea surface; and 3) Isla Las Animas.

Both individuals and schools of *Sphyrna lewini* were seen. Generally the sharks within schools swam in a polarized manner, remaining relatively equidistant from each other and swimming forward and changing direction together (Figure 2A, B). For the purposes of data sampling, sharks were counted during discrete "observation dives," which usually consisted of free dives, but included some observations from the surface. Scalloped hammerheads were encountered on 91% of the free dives at El Bajo, 58% at Isla Las Animas, and 34% at Las Arenitas Rocks. These percentages are a rough index of relative abundance because they are probably affected by differences in search success and water clarity. School sizes at El Bajo were larger than those at Las Arenitas Rocks and Isla Las Animas, but no large difference existed between group sizes at Las Arenitas Rocks and Isla Las Animas.

The number of scalloped hammerhead sharks in the vicinity of El Bajo was estimated by using the

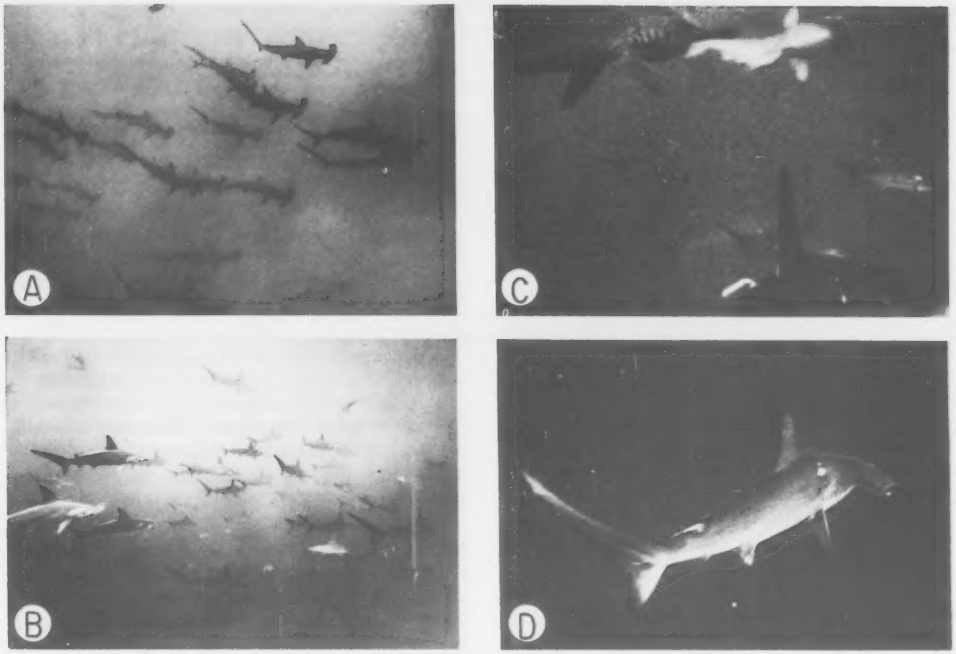

FIGURE 2.—Scalloped hammerhead sharks photographed in the Gulf of California: A. Hammerhead school as viewed obliquely from below. Note leading edge of school, orientation of sharks in same direction, and similar spacing between sharks. B. Side view of school. C. Shark in upper right-hand corner performing headshaking behavior. Note shark with color-coded streamer tag beneath headshaking shark. D. Female hammerhead possessing ellipsoid scar (above last gill slit), possibly inflicted during courtship.

Lincoln Index capture-recapture analysis, modified for observational data. On the morning of 3 August, 21 sharks were tagged with color-coded, plastic-streamer dart tags. Upon spear application of the tags, the sharks often accelerated momentarily, but usually remained within their groups. That afternoon, 9 tagged sharks were observed again within a group of 225, yielding an estimate of 525 sharks in the seamount vicinity (2-4 ha). We feel that this estimate was unbiased because all 21 of the tagged sharks dispersed among various groups after tagging.

We observed groups of 3 to 225 scalloped hammerhead sharks per dive with a mean of 19 (Table 1). Groups of sharks were encountered on 83% of the dives, two sharks on 7%, and single shark on 20% of the dives. Group size varied greatly; this in part reflected the dynamic composition of the groups as sharks left and returned. This was tested by noting the number of sharks associated with a tagged shark when it was reobserved. Tagged sharks (39 were tagged at El Bajo over the study period) were reobserved with varying numbers of accompanying sharks. For example, shark no. 19 was reobserved on four occasions during 135 min on the morning of 6 August with successive groups of 50, 15, 100, and 10 sharks. Such dynamics also were evident to an observer who remained for 120 min above one large group, which varied over that time from 50 to 225 sharks. Subgroups of up to 50 sharks departed and returned to this main group. Groups either appeared to remain at one certain spot (e.g., just upcurrent of the seamount at El Bajo) or repeatedly to follow a path within a relatively small area (ca. 2 ha). At Las Arenitas Rocks a group of ca. 50 scalloped hammerheads repeatedly traveled a particular oblong circuit once each 15 min.

There appeared to be some departures of sharks from El Bajo. Although 16 of the 21 sharks tagged the morning of 4 August were reobserved later

TABLE 1.—School size, depth, shark length, and sex composition of schools of scalloped hammerhead sharks at Las Arenitas Rocks, El Bajo Espiritu Santo, Isla Las Animas, and all locations in the Gulf of California. Numbers in parentheses refer to numbers of observations.

Descriptive categories	Las Arenitas Rocks	El Bajo	Isla Las Animas	All locations pooled
[1]School size, no.:				
Mean (*n*)	12(128)	44(54)	11(43)	19(225)
Maximum	100	225	50	225
[2]Individuals depth, m:				
Minimum	.6	.6	.6	.6
Mean (*n*)	10.1 (114)	10.7 (43)	11.7 (43)	10.4 (200)
Maximum	22.7	22.7	22.7	22.7
Variation around mean	4.3 (6)	8.5 (11)	3.1 (4)	6.7 (21)
Total length, m:				
Minimum	.9	.9	.9	.9
Mean (*n*)	1.6 (39)	1.8 (28)	1.7 (7)	1.7 (74)
Maximum	2.3	3.4	2.4	3.4
Sex ratios:				
Male:female (*n*)	1:1.6 (63)	1:3.8 (84)	1:3.1 (65)	1:2.7 (212)

[1]School defined as three or more sharks.
[2]Individuals' mean and maximum depths based only on observable sharks, since at times (particularly at El Bajo) schooling sharks extended to depths beyond our vision.

that day, only 5 were reobserved 2 d later, despite the fact that an equivalent amount of searching was conducted. The possibility of such migratory or dispersal movements was supported by the occasional observation of single scalloped hammerhead moving slowly at the surface over deep water between islands.

The mean depth of the schooling individuals was 10.4 m with sharks as shallow as 0.6 m and as deep as 22.7 m (Table 1). Depths were estimated with the aid of wrist-worn depth gages. Small groups of sharks were seen swimming close to the sandy or rocky substrate and at times appeared to explore rocky crevices.

The scalloped hammerhead schools were composed of sharks of variable size; both sexes were present in a school, but females were more common (Table 1). The largest individuals, which appeared to be females, often remained at the top of the schools. The sharks at El Bajo were larger than those at Las Arenitas Rocks, but no difference existed between those at El Bajo and Isla Las Animas and at Las Arenitas Rocks and Isla Las Animas. Females were more prevalent at all three sites with male:female ratios ranging from 1:3.8 at El Bajo to 1:1.6 at Las Arenitas Rocks (Table 1).

Within the groups, sharks performed a number of behavior patterns, including the following (in order of decreasing frequency): 1) tilting the body laterally; 2) accelerated swimming with headshaking (Figure 2C); 3) accelerated swimming, dorsal or ventral surface upward, while thrusting the midsection; 4) accelerated corkscrew swimming, rotating 360° around the longitudinal axis; 5) hitting of conspecific with the snout; 6) jaw opening; and 7) clasper flexion. Headshaking has been observed previously in wild hammerheads by Herald[1]; hitting, jaw opening, and clasper flexion resemble behaviors observed in captive bonnethead, *S. tiburo* (Myrberg and Gruber 1974).

Sharks of all sizes and both sexes performed tilting. This generally occurred when a diver was swimming above or behind the shark, perhaps enabling the shark to see the diver better. In one instance, while tilting, a shark flexed his clasper in the direction of an adjacent conspecific. Six males and three females varying from 1.5 to 1.8 m long were observed headshaking. Medium-sized sharks also performed corkscrewing; the sex of the single shark identified was male. Although jaw opening, apparently directed at divers, occurred in sharks outside of groups, headshaking, midsection thrusting, and corkscrewing usually occurred within the group, often at long distances from the diver. On two occasions sharks followed headshaking and corkscrewing by hitting their snouts against adjacent individuals, lateral or anterior to the first dorsal fin.

Many sharks bore abrasions (Figure 2D). These were small, recently inflicted, whitish patches (estimated diameter 4-8 cm), or partially healed black patches. In 21 out of 27 sharks, these were located lateral or anterior to the first dorsal fin, and if two patches were present, at times appeared bilaterally symmetrical. Possessors were predominately female (23 out of 27) and ranged from 1.2 to 2.1 m long ($\bar{x}$ = 1.7 m). These scars may be inflicted by males during mating. Captive, small

[1]Herald, E. The shimmy behavior of the hammerhead shark. Unpubl. manuscr., 4 p. Steinhart Aquarium, San Francisco, Calif., available from authors.

male bonnetheads accelerated from a position just above and behind a large female and scraped her dorsum between the first and second dorsal fins with their heads, often leaving similar scrapes (Myrberg and Gruber 1974). Bite scars, often consisting of a row of teeth marks, are inflicted during courtship in some sharks (Stevens 1974; Klimley 1980). The presence of these scarred females raises the possibility that the scalloped hammerhead schools may have a reproductive function. Grouping for reproduction has been speculated for *Galeorhinus australis* (Olsen 1954) and *Squalus acanthias* (Jensen 1965).

Other functional possibilities for the schooling include: 1) migration (Olsen 1954; Kenney 1968), 2) protection from predation (Barlow 1974), and 3) cooperative location or capture of prey (Coles 1915; Bigelow and Schroeder 1948). Other than the departure of tagged sharks from El Bajo, little evidence for or against the first hypothesis can be marshalled. The second hypothesis seems unlikely due to the absence of known predators. We do, however, have some evidence against the last hypothesis. Feeding was not observed, although scalloped hammerheads were often swimming through large schools of fishes. No feeding responses were directed at baits placed either among or above large numbers of scalloped hammerheads. Although fishing was carried out continuously, only a single male was captured. Feeding readiness was also tested by playing back sounds, attractive to many species of sharks including *Sphryna* sp. (Nelson and Johnson 1972), and baiting immediately after encountering grouped sharks. In 20 min of sound playback and 125 min of baiting, only a single shark was attracted. The phenomenon of grouped hammerhead sharks presents a unique opportunity for the further understanding of shark social behavior, since the sharks are found in sufficiently clear water for observation, shallow enough for free diving, remain in a sufficiently limited area for prolonged observations, and tolerate the approach of divers.

Acknowledgments

The authors thank J. McKibben, G. Pittenger, T. Rulison, and J. Sullivan for assistance in data acquisition. Flip Nicklin organized the cruise with financial support from National Geographic Magazine. The *Juan de Dios Batiz*, a research vessel of the Centro Interdisciplinario de Ciencias Marinas, La Paz, was kindly made available for the study by the director, D. Lluch Belda. Photographs in Figure 2 were taken by Jim McKibbn, F. Nicklin, and D. Nelson. Partial support was provided by ONR contract N00014-77-C-0113 to the second author.

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CLEANING SYMBIOSIS BETWEEN TOPSMELT, *ATHERINOPS AFFINIS*, AND GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, IN LAGUNA SAN IGNACIO, BAJA CALIFORNIA SUR, MEXICO

Many species of marine fishes are known to engage in various forms of cleaning symbiosis (Limbaugh 1961; Hobson 1969, 1971). The cleaners, generally small or juvenile fish, remove ectoparasites and necrotic tissue from larger host fish. This promotes the well-being of the host and provides food for the cleaner. Cleaning symbiosis between topsmelt, *Atherinops affinis*, cleaners and gray whale, *Eschrichtius robustus*, hosts was observed during the author's study of breeding gray whales in Laguna San Ignacio, Baja California Sur, Mexico, supported by the United States Marine Mammal Commission, the National Geographic Society, and the World Wildlife Fund-U.S. (Swartz and Jones[1]). Topsmelt are perennial residents of the lagoon and gray whales occupy the lagoon for 3 to 4 mo each winter. As we photographed gray whales from our skiff, schools of topsmelt were seen accompanying the whales and picking at clusters of parasitic barnacles, *Cryptolepas rhachianecti*, and whale lice, *Cyamus* sp., which incrust these cetaceans (Rice and Wolman 1971).

Topsmelt in association with gray whales were collected during the 1978-79 winter with a "mackerel rig" consisting of 1 m of monofilament line with four No. 6 brass hooks spaced 10 cm apart. The standard length (SL) of each fish was measured and its gut contents examined. A second series of topsmelt were collected during the same winter in the absence of gray whales.

The topsmelt ranged from 17 to 29 cm SL. All 38 specimens collected in association with gray whales contained bits of sloughed gray whale epidermis and whale lice appendages. No barnacle appendages or other material was found in these fish. None of 25 topsmelt collected in the absence of whales contained any gray whale epidermis or whale lice; rather they contained bits of filamentous brown algae, *Ectocarpus* sp., and gammarid amphipods.

Topsmelt are described as opportunistic feeders on marine plants, small crustaceans, bryozoans, and hydroids (Frey 1971). During the breeding season of the gray whale, topsmelt in Laguna San Ignacio supplement their diets by cleaning slou - ing epidermal tissue and external parasites from gray whale hosts.

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MORPHOLOGICAL FEATURES OF THE OTOLITHS OF THE SAILFISH, *ISTIOPHORUS PLATYPTERUS*, USEFUL IN AGE DETERMINATION[1]

Because of its spectacular runs and leaps, sailfish, *Istiophorus platypterus*, is highly valued by sport fishermen, and the fishery contributes substantially to the economics of coastal regions (de Sylva 1969). However, information on the biology of sail-

[1]Swartz, S. L., and M. L. Jones. 1978. Gray whales, *Eschrichtius robustus*, during the 1977-1978 and 1978-1979 winter seasons in Laguna San Ignacio, Baja California Sur, Mexico. Available Natl. Tech. Inf. Serv., Springfield, Va., as PB-289 737, 35 p.

fish, even though critical to resource management, is limited.

Age estimates and growth rates are necessary to prepare accurate stock statistics. Age determinations in fish are generally indirect measures and are made from length-frequency analyses (Petersen's method) or annual events in hard tissue (Bagenal 1974). The length-frequency method has been applied to sailfish (de Sylva 1957; Koto and Kodama 1962), but the results are inconclusive at best. Annual events recorded in hard tissues are a more accurate method of age determination, and Jolley (1974, 1977) counted the rings in dorsal fin spines to estimate the age of sailfish. The length-frequency data (de Sylva 1957; Koto and Kodama 1962) and proposals of Maksimov (1971) from length-frequency data indicated a rapid growth rate and relatively short lifespan of 3-5 yr for a sailfish. Jolley's (1974) analysis also indicated a rapid growth rate but a possible lifespan of about 10 yr, so at present, age determination in sailfish is unresolved.

Otoliths have been shown to be accurate indicators of age (Bagenal 1974; Six and Horton 1977) and are particularly useful on species of fish which lack scales or have minute scales such as those species in the family Istiophoridae. Otoliths are composed of calcium carbonate in the form of aragonite (Irie 1955; Degens et al. 1969) and are formed in the labyrinth of teleost fish. There are three otoliths (sagitta, lapillus, and asteriscus) on each side of the brain cavity in the inner ear (Lowenstein 1971) and the morphology of these calcified structures is species specific (Hecht 1978; Morrow 1979). The sagitta is usually the largest otolith and the one most often used for age determinations, but the other two otoliths have not been adequately studied and might also be of use. The otoliths of sailfish and other billfishes (families Istiophoridae and Xiphiidae) have been thought to be so small that they would not be useful in age determinations (Jolley 1974; Beckett 1974). Consequently, age and growth data are lacking for these important recreational and commercial species. In this study we analyzed 65 sailfish and described the morphology of the otoliths. A mathematical relationship between the wet weight of the fish and morphological features of the sagitta, enabled us to estimate the age of all but one specimen. Ages of very large fishes, previously difficult to measure, were readily amenable to otolith age analysis.

Methods

Otoliths were collected from sailfish at taxidermy facilities in Florida in fall 1978. Total lengths (TL) and wet weights were recorded from the tags placed on the fish at the dock and otoliths were extracted from 65 fish. The otoliths of sailfish were extremely small and required careful dissection. A saggital cut was made on the midline of the head and the semicircular canals dissected from the brain area. All three otoliths were removed from the semicircular canals and cleaned. Dried otoliths were attached to aluminum stubs; gold-coated otoliths were viewed in a Cambridge Stereroscan Mark 2A[2] scanning electron microscope (SEM).

The internal structure of the sagitta was observed by attaching the sagitta to a SEM stub with 5 min epoxy and fracturing it through the core region. The fractured otoliths were etched for 5 min in 7% ethylenediaminetetraacetic acid (pH 7.4) and then coated with gold before viewing. The lapilli of sailfish were viewed with reflected light microscopy to determine if this would be a viable alternative to SEM preparations.

Results

The morphological nomenclature we use to describe sagitta is that of Hecht (1978) and Morrow (1979). The otoliths are extremely small, from 0.75 to 1.5 mm long. The medial or concave surface (Figure 1) has a deep and well-defined sulcus and the depth of the sulcus increased with fish weight. The sagitta has no collum and lacks anterior and posterior cristae. The excisural notches are distinct and V-shaped and have two lobes which fold onto each other. The antirostrum is one-third as long as the rostrum and well separated from the rostrum. Consequently sagitta had a different configuration from most sagitta, as the rostrum is exaggerated. The surface of the concave portion of the sagitta is granular with crystalline palisade configurations.

There are distinct ridges on the side of the rostral lobe (Figure 2) which we interpret as annual events, as there is an increase in ridge number with weight (Figure 3). The sagitta of a sailfish

[1]Contribution No. 397 of the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina.

[2]Reference to trade names doesnot imply endorsement by the National Marine Fisheries Service, NOAA.

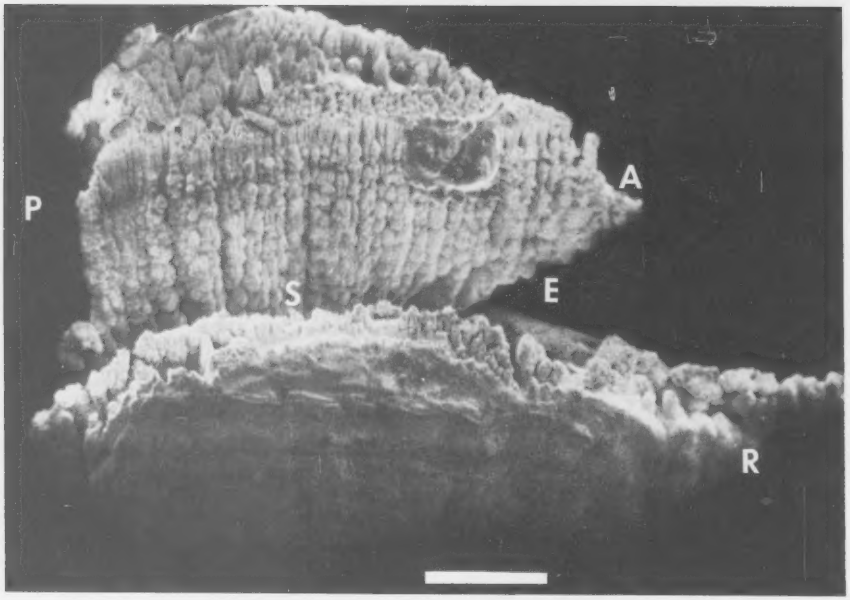

FIGURE 1.—The concave medial surface of the left sagitta from a sailfish that weighed 27.7 kg (18×): A, Antirostrum; E, Excisural notch; S, Sulcus; P, Posterior. Bar = 0.5 mm.

FIGURE 2.—Rostral lobe of the left sagitta of a 27.7 kg sailfish (60×). Numbers indicate ridges. Bar = 0.1 mm.

that weighed 27.7 kg and was 226 cm TL had 7 ridges (Figure 2), while the sagitta of a sailfish that weighed 12.7 kg and was 183 cm TL had 3 ridges (Figure 4). These ridges are distinctive and easily counted, and of a sample of 65 sailfish only 1 specimen had uncountable ridges on both sagittae.

The convex or lateral surface of the sagitta (Figure 5) was moderately smooth and the two lobes were joined in the core region. The convex surface did not have the distinctive configuration seen on the side of the rostral lobe. A medial section of the sagitta revealed internal structures which indicated incremental otolith growth and progressive deposition (Figure 6).

The asteriscus and lapillus (Figure 7) are much smaller than the sagitta and also show internal features that appear to have progressive deposition. The asteriscus is very fragile and was often broken during dissection, but its growth features support the sagittal ridge counts. The lapillus was much heavier in structure than the asteriscus and also showed internal growth features that appear to be age related (Figure 8). The lapillus showed layers that correspond to the number of ridges found on the sagitta when viewed under transmitted light (Figure 9). The lapilli age counts were identical to sagittal ridge counts 85% of the time and ±1 yr in the other counts. The possibility exists that age estimates could be obtained by light microscope techniques, although the sagittal ridges were very distinct in SEM preparations which we feel would be more accurate.

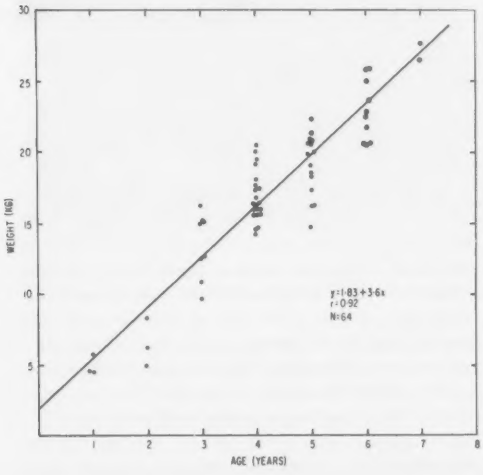

FIGURE 3.—Relationship between the weight of the sailfish and the number of ridges (years) on the sagitta.

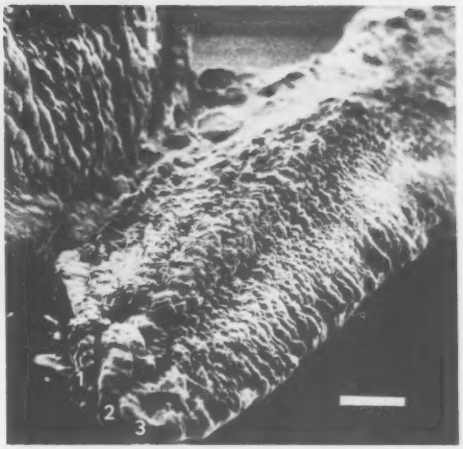

FIGURE 4.—The rostral lobe of the left sagitta from a 12.7 kg sailfish with three ridges (85×). Numbers indicate ridges. Bar = 0.1 mm.

The ridges on the sagitta of 64 sailfish were counted and compared with body weight and a strong correlation was found (Figure 3). The ridges appear to be annual events and fish with four ridges were the most numerous in our sample. We did a log transformation of the allometric growth curve equation or power curve fit of the data (Table 1) so we could compare our data directly with that of Jolley (1977) for which summary statistics only are available. The data used for statistical analysis were selected from the Jolley (1977) regressions. An F-test for difference between the regression coefficients gave $P>0.05$, so there is no apparent difference between the slopes of Jolley's data and ours. The data indicate that the sailfish develop a large muscle mass in a short period of time (<4 yr), and our results are similar to Jolley's over the same time span.

TABLE 1.—Age-weight relationships ($Y = ax^b$) for the Atlantic sailfish as expressed by predictive power equations, $\log_{10}$ transformed for purposes of testing difference in regression coefficients between the data presented in this paper and those of Jolley (1977).

Source	N	Regression coefficient	Y-intercept	r	P (F-test)
Present study	64	0.883	4.64	0.86	>0.05
Jolley (1977):					
Males	74	.888	1.48	.85	>0.05
Females	73	1.048	1.33	.88	>0.05

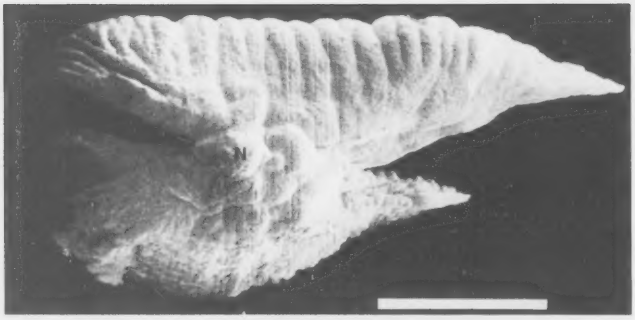

FIGURE 5.—The convex distal surface of the left sagitta of a 27.7 kg sailfish; N indicates nuclear (core) region (18×). Bar = 1 mm.

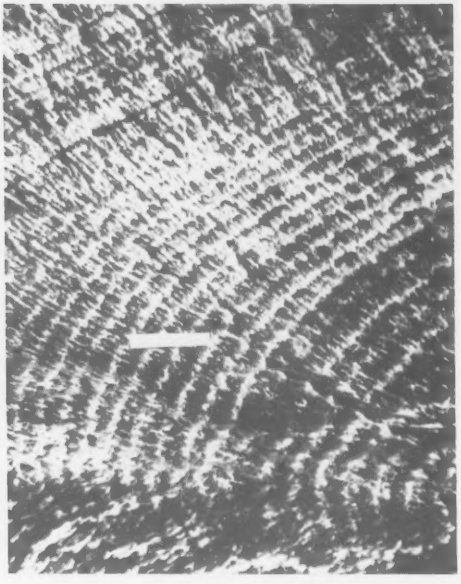

FIGURE 6.—Cross section of the rostral lobe of a sailfish sagitta that shows incremental growth in the internal structure (1,100×). Bar = 10 μm.

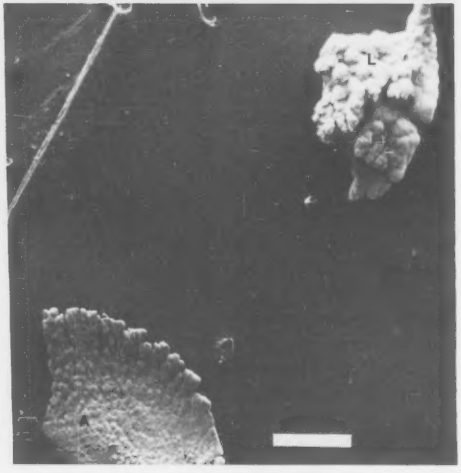

FIGURE 7.—The left lapillus (L) and asteriscus (A) of a 27.7 kg sailfish (18×). Bar = 0.5 mm.

Discussion

The otoliths from sailfish are very small in relation to the size of the fish and appear to be unique, as their prominent ridges on the rostral lobe are different from the morphology of other teleost otoliths. For comparison of morphological features, excellent surveys of otoliths from a broad range of families and geographic areas are found in Hecht (1978) and Morrow (1979). The external ridge feature makes it possible to use the sagitta of the sailfish for determination of age and growth rates.

de Sylva (1957) proposed that sailfish average 183 cm TL and attain an average weight of 10 kg at the end of the first year, but the Petersen's method which he used has several limitations (Watson 1964). It is most suitable for fish in their early life, with species that have a short annual spawning period, and large samples are required as individuals cannot be aged. The biology of sailfish does not lend itself to analysis by the Petersen technique. This was recognized by Jolley (1974, 1977), who utilized hard parts (dorsal spines) for age determinations. Our estimates of growth rates and age estimates are similar to his. However, Jolley (1977) found that only 24% of the samples

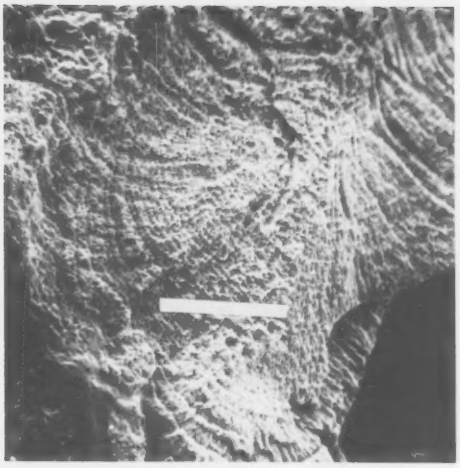

FIGURE 8.—The internal structure of the lapillus of a 20.5 kg sailfish (400×). Bar = 50 μm.

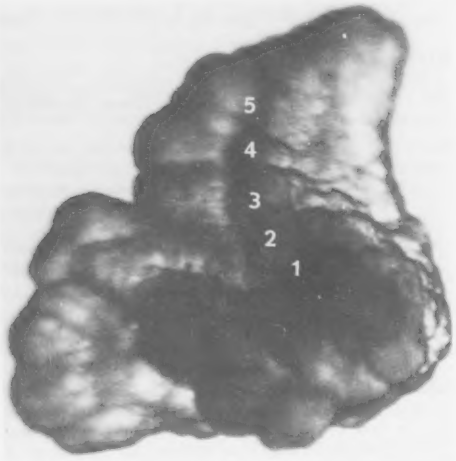

FIGURE 9.—The lapillus of a 20.5 kg sailfish viewed under transmitted light. Five layers are shown (40×).

he examined could be aged by the spine analysis, and it was particularly difficult for him to age larger specimens, while we read 64 of 65, or 98%, of the otoliths. Our percentage might be lower for a larger sample or older fish, but an age estimate was usually possible from one of the two sagitta present in the fish. We did not find it difficult to resolve the age of our largest specimens.

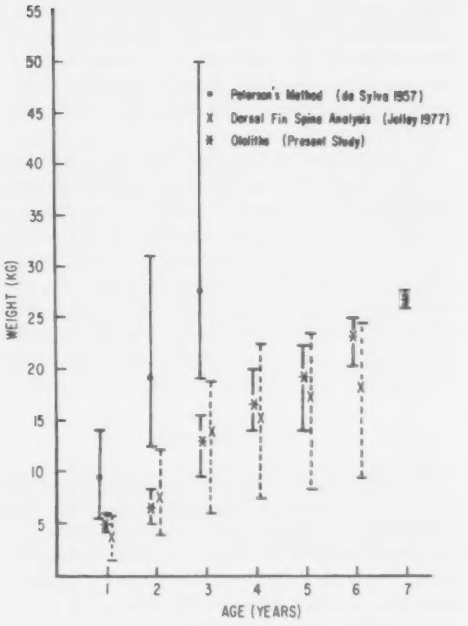

FIGURE 10.—Comparison of relationships between the mean weight of sailfish and estimated age. Bars represent ranges.

The age-weight relationship developed in our study from otoliths, and by Jolley (1977) from analysis of dorsal fin spines (Figure 10) indicates that weight attained at ages 1 through 3 are about 50% less than those estimated by de Sylva (1957) and Koto and Kodama (1962). Tag data (Mather et al. 1974) are inconclusive due to the small number of returns. Our two largest specimens (estimated age 7) weighed 26.4 and 27.7 kg and were 228.6 and 226.1 cm TL. This is similar to Jolley's largest fish of 26 kg at our equivalent age 6, but his larger fish could not be aged with the fin spine method.

Sailfish are multiple spawners (Jolley 1977), which could account for the range of weights in the different age-groups. A study of internal patterns in otoliths might make it possible to determine when an individual fish spawned. The internal microstructure could be a permanent calendar of the physiological history of the fish. Further study on the micromorphology and internal structure of the otolith should reveal valuable information. The internal increments occurred at a frequency of 13 or 14 increments in each major assemblage which could be evidence of a lunar periodicity.

Hence, we had additional confidence in our interpretation of the ridges as annual events and since ridges were easier to count, we used them in our age determinations. Further analysis might show daily increments (Pannella 1974) within the lunar increments.

In conclusion, we have been able to collect the otoliths of sailfish, and all three otoliths showed morphological features that can be readily observed. The internal and external otolith structures, viewed with SEM, appeared to show an annual periodicity and provided data that are not available by other means. With this data it is possible to determine a growth rate and age estimate for all sizes of the sailfish sampled, including larger fish that were difficult to age in the past.

Acknowledgments

We wish to thank Vern Barber and the Scanning Electron Microscope Laboratory at Memorial University, St. John's, Newfoundland, Canada, for the use of the SEM and help in specimen preparations. We thank J. T. Reese Company, Ft. Lauderdale, Fla., and the Pflueger Taxidermy Co., Hallandale, Fla., who made the fish available, for their generosity and assistance. Without their cooperation, this study would not have been possible. We appreciate the support of R. Macon and R. Feller's constructive comments on the manuscript and his assistance with the statistical analysis. This work was supported by a Visiting Fellowship from the National Research Council of Canada to the senior author and a grant from the Research and Productive Scholarship Fund of the University of South Carolina to J. M. Dean.

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DIEL AND SEASONAL MOVEMENTS OF WHITE STURGEON, *ACIPENSER TRANSMONTANUS*, IN THE MID-COLUMBIA RIVER

The white sturgeon, *Acipenser transmontanus*, is a commercial and sport fish common to major river systems of the Pacific Coast from Monterey, Calif., to Alaska (Scott and Crossman 1973). However, there is considerable confusion concerning migration habits or seasonal movements of the species. Early workers (Jordan and Evermann 1908; Craig and Hacker 1940) considered white sturgeon anadromous. In free-flowing rivers, white sturgeon move upstream in spring prior to spawning (Carl et al. 1967; Bell 1973). Other investigators (Bajkov 1951) suggested seasonal movements in the lower Columbia River may be related to feeding.

Although some white sturgeon can be found in the ocean and may ascend rivers to spawn, the species is not truly anadromous. Many individuals remain in freshwater, and those found in the upper Columbia River and its tributaries are landlocked by a system of hydroelectric dams. However, permanent freshwater residents also show seasonal movements. Studies in 1975 and 1976, involving radio-tagged white sturgeon in the mid-Columbia River, indicated sturgeon movements >2 km occurred when river temperatures exceeded 13° C (Haynes et al. 1978). Furthermore, size and possibly sexual maturity influenced direction of movement in the river. Smaller white sturgeon moved downstream in summer, larger sturgeon moved upstream in summer and fall, and intermediate-sized sturgeon remained near release points. Although seasonal movements may be related to water temperature, no quantitative data exist on diel activity patterns of the species. To further evaluate seasonal movements in the free-flowing Hanford reach of the Columbia River, we fitted additional white sturgeon with radio transmitters in spring and early summer 1977 and continued monitoring fish which had been tagged in 1975 and 1976.

Methods

Radio-telemetry equipment was developed by the University of Minnesota, Bioelectronics Laboratory (Tester and Siniff[1]). Nineteen white sturgeon ranging from 98 to 236 cm total length were captured with trammel nets and angling gear at White Bluffs Pool (Figure 1), about 48 km upstream from Richland, Wash. Transmitters were selected so as not to exceed 2% of estimated sturgeon body weight and were attached dorsally (Haynes et al. 1978). Twelve transmitters had temperature sensors (precision ±0.2° C, Kuechle[2]). An automatic, channel-scanning receiver and recording station, capable of sequentially monitoring 16 channels, was established at White Bluffs Pool to record environmental temperatures and sturgeon movements in and out of the pool. Receivers operated on a carrier frequency of 53 MHz

[1]Tester, J. R., and D. B. Siniff. 1976. Vertebrate behavior and ecology progress report for period July 1, 1975-June 30, 1976. COO-1332-123. Prepared for U.S. Energy Research and Development Administration. Contract No. E(11-1)-1332 by Univ. Minn., Minneapolis, 63 p.

[2]V. B. Kuechle, Bioelectronics Laboratory at Cedar Creek, University of Minnesota, Minneapolis, pers. commun. 1977.

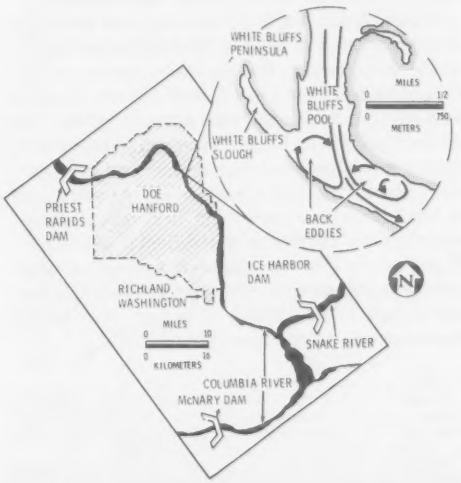

FIGURE 1.—White Bluffs monitoring area for white sturgeon movements in the Columbia River.

and were capable of distinguishing 100 discrete crystal-tuned transmitters. Sturgeon, including those radio-tagged in 1975 and 1976 (Haynes et al. 1978), were located once or twice per week with boat- and truck-mounted receiver gear. On several occasions, sturgeon locations were monitored manually over a 24-h period.

During the summer we measured Columbia River temperatures at numerous midchannel locations from Priest Rapids Dam to Richland, 95 km downstream (Figure 1). On these occasions river temperatures only varied about 1° C. Therefore, mean river temperatures (standard deviation = 0.5° C/d) during the study were calculated from 12 temperature readings taken daily at Priest Rapids Dam. Daily mean river temperatures were averaged weekly. Main current temperatures in White Bluffs Pool were monitored by a reference temperature transmitter in the pool and were also measured while tracking fish.

Analysis of variance was used to compare mean sturgeon environmental temperatures in six time periods (0200-0600, 0600-1000, 1000-1400, 1400-1800, 1800-2200, and 2200-0200 h) with the weekly mean river temperature from 19 June to 20 August 1977. Differences between sturgeon environmental temperatures and weekly average river temperatures were experimental units within each time period. Honest significant difference (HSD) tests (Snedecor and Cochran 1972) were used to establish which periods differed.

White Bluffs Pool is 1.5 km long and has three distinct habitats (Figure 1). Most of the pool is part of the deep, swiftly flowing main current of the Columbia River and has a rock bottom. A deep, slow-moving back eddy with a sandy bottom lies off the tip of White Bluffs Peninsula. White Bluffs Slough has a mud and rock bottom and extends 1 km upstream along the peninsula. The pool ranges in depth from 1 m in the slough to 20 m in midpool, and the main current is well mixed (Gray et al.[3]; Page et al.[4]). However, underground spring seepage areas, common in the region, are 1°-5° C lower, and slough areas are 2°-5° C higher, than mixed main currents in summer (Haynes 1978).

[3]Gray, R. H., T. L. Page, and E. G. Wolf. 1976. Report on aquatic ecological studies near WNP-1, 2, 4, Sept. 1974-Sept. 1975. WPPSS Columbia River ecology studies, Vol. 2, 115 p. Battelle, Pac. Northwest Lab., Richland, Wash.

[4]Page, T. L., R. H. Gray, E. G. Wolf, and M. J. Schneider. 1976. Final report on aquatic ecological studies conducted at the Hanford Generating Project 1973-74. WPPSS Columbia River ecology studies, Vol. 1, 206 p. Battelle, Pac. Northwest Lab., Richland, Wash.

Results and Discussion

Main current temperatures in White Bluffs Pool averaged within 0.5° C of Priest Rapids Dam temperatures and weekly standard deviations averaged 0.3° C throughout 1977. Therefore, deviations in daily and weekly midriver temperatures were small relative to temperature differences in spring seepage and slough areas in summer. Throughout the summer of 1977, individual sturgeon with temperature transmitters engaged in movements that often resulted in a 2°-4° C daily change in recorded temperature. The analysis of sturgeon environmental temperatures versus weekly average river temperatures during certain periods of the day (Table 1) indicated significant differences ($P<0.001$). Because deviations in main river temperatures were 8-25% less within and between days than changes in sturgeon environmental temperatures, recorded temperature changes indicated sturgeon moved into areas of differing environmental temperatures. Position determinations confirmed these movements and indicated sturgeon generally occupied midchannel areas from early morning until midafternoon. Movements into nearshore and slough areas were observed in late afternoon and evening.

During summer 1977 from 0200 to 1000 h, sturgeon environmental temperatures (Figure 2) were somewhat, but not significantly, lower (−0.35° C) than weekly average river temperatures, suggesting presence in deeper, and possibly spring-fed areas. During 1400-2200 h, sturgeon environmental temperatures were significantly ($P<0.05$ by HSD) higher (0.85° C) than the weekly average river temperature, indicating presence in warmer, shallow slough areas. During 1000-1400 h and 2200-0200 h, sturgeon environmental temperatures were somewhat higher (0.32° C) than the weekly average, suggesting transition periods when sturgeon moved between inshore and midchannel areas.

Although changes in sturgeon environmental temperatures documented movements among

TABLE 1.—Analysis of variance on differences in mean sturgeon environmental temperatures in six daily time periods (0200-0600, 0600-1000, 1000-1400, 1400-1800, 1800-2200, and 2200-0200 h).

Source	df	SS	MS	F
Among time periods (diel)	5	164.67	32.93	47.7**
Within time periods	701	485.28	0.69	
Total	706	649.95		

**$P<0.001$.

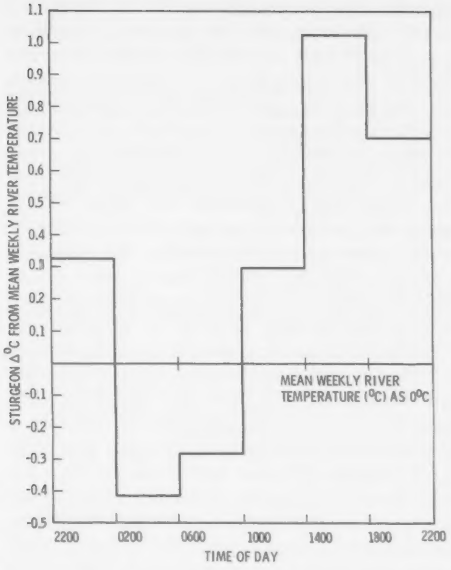

FIGURE 2.—Mean sturgeon environmental temperature deviation (Δ° C) from mean weekly Columbia River temperatures averaged over 4-h periods within the diel cycle, from 19 June through 20 August 1977.

habitats, we do not believe temperature differences in White Bluffs Pool caused diel sturgeon movements. Rather, diel movements are probably influenced by light. Movement to cool, deep areas occurred prior to sunrise and movement to warm, shallow areas peaked after sunset. Sturgeon were sensitive to light when captured for tagging and remained active until a towel was placed over their eyes. Bait angling for sturgeon was most successful during sunset and sunrise, and netting near shore was most productive at night. Evening movements to back eddy and slough areas of White Bluffs Pool, where benthic organisms and smaller fish are more abundant, may be related to feeding.

Sturgeon are bottom feeders and in freshwater reportedly eat crustaceans (*Daphnia* and copepods), molluscs (clams and snails), insect larvae (chironomids, stone flies, and ephemeropterans), and fish (Bajkov 1949; Semakula and Larkin 1968). Sturgeon in the mid-Columbia River at Hanford ingest crayfish, fish (including whitefish, suckers, and sculpins), midge and caddis fly larvae, snails, and periphyton (Gray et al. footenote 3; Page et al. footnote 4).

Daily environmental temperature records indicated sturgeon did not consistently engage in a diel movement pattern. Sturgeon sometimes spent one or more days in cooler, midchannel areas. Occasionally, sturgeon remained near inshore areas through midday, although variability within and among fish was common.

Haynes et al. (1978) suggested long-distance sturgeon movements in the mid-Columbia River were related to temperature. Data collected in 1977 confirm these observations. Sturgeon movements >2 km up- or downriver began in early summer when river temperature rose to 13° C and ended in fall when temperature dropped below 13° C (Figure 3).

The possibility that photoperiod plays a role in initiation of long-distance movement and termination of movement appears unlikely. Pacific Northwest drought conditions in 1977 resulted in extremely low Columbia River flows and higher-than-normal water temperatures. River temperatures in 1977 did not drop below 13° C until early November, and sturgeon movements continued throughout. In previous years, river temperatures

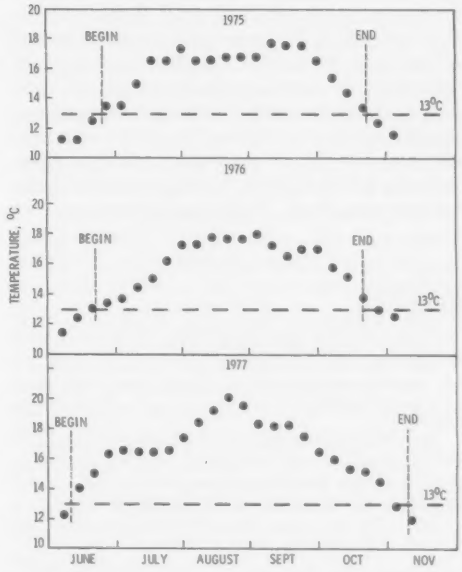

FIGURE 3.—Beginning and end of sturgeon movement (>2 km up- or downstream from release site) versus weekly average Columbia River temperatures in 1975 and 1976 (derived from Haynes et al. 1978) and 1977.

declined below 13° C and sturgeon movements ceased by mid-October. If photoperiod were involved, sturgeon movements in 1977 should have stopped at about the same time as they did in 1975 and 1976. Complete cessation of movement >0.5 km in autumn may be related to cold-induced inactivity.

Linear regression analyses comparing distances moved by sturgeon with river flows at Priest Rapids Dam produced scatter diagrams with regression coefficients approaching zero. In contrast to results of studies in the Snake River, Idaho (Coon et al.[5]), river flow apparently had no influence on long-distance sturgeon movements in the Columbia River at Hanford.

The complex interaction of water temperature, light cycle, feeding, urge to spawn, and other factors undoubtedly influence sturgeon movements in the mid-Columbia River. Although temperature is a major influence stimulating seasonal movements, light cycle and feeding probably influence diel movements.

Acknowledgments

We thank C. D. Becker, who critically reviewed the manuscript; and R. P. Olson, S. W. Cubberly, D. W. Crass, and R. W. Cordo, who assisted data collection in the field. V. B. Kuechle, Bioelectronics Laboratory at Cedar Creek, University of Minnesota, kindly provided information on temperature transmitter precision. The study was supported by the U.S. Department of Energy under Contract EY-76-C-06-1830 with Battelle Memorial Institute, Pacific Northwest Laboratories.

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FEEDING PERIODICITY AND DIEL VARIATION IN DIET COMPOSITION OF SUBYEARLING COHO SALMON, *ONCORHYNCHUS KISUTCH*, AND STEELHEAD, *SALMO GAIRDNERI*, IN A SMALL STREAM DURING SUMMER

Throughout their native range in northwestern North America, juvenile coho salmon, *Oncorhynchus kisutch*, and steelhead, *Salmo gairdneri*, occur sympatrically in streams (Milne 1948). In these instances, social interaction between the two species leads to spatial segregation during the spring and summer, with coho salmon generally occupying pools and steelhead riffles (Hartman 1965; Allee 1974). A recent investigation of naturalized populations in the Great Lakes region has observed similar patterns of spatial segregation (Johnson and Ringler 1980).

It is generally accepted that social interaction among closely related fish species may lead to interactive segregation, with each species segre-

gating into a habitat which it is best suited to exploit (e.g., Nilsson 1967). In this respect, interactive segregation of juvenile coho salmon and steelhead enables the surface and drift forager, coho salmon, to inhabit pools and the more bottom-oriented steelhead to occupy riffles. Johnson and Ringler (1980) pointed out that in sympatry with coho salmon, steelhead are found in areas (riffles) where the standing crop of benthic invertebrates is the greatest, an obvious advantage in conjunction with their benthic habits. Conversely, coho salmon which feed predominantly from the drift presumably have a relatively long time interval in which to observe drifting prey because of decreased water velocities in pools.

Johnson and Ringler (1980) demonstrated that in sympatry the diet of subyearling coho salmon was closely associated with the composition of the drift, and the diet of subyearling steelhead was more closely associated with the bottom fauna. They found a low degree of overlap in the diurnal summer diet of coho salmon and steelhead due to the utilization of drifting terrestrial invertebrates by coho salmon and benthic invertebrates by steelhead. They speculated that since the composition of invertebrates on or within the substratum of a stream is much more stable over a 24-h period than the composition of the invertebrates drifting over it, that the diet of the drift feeder (coho salmon) would be more variable than the diet of the benthic forager (steelhead) over a 24-h period. The purpose of this study was to test this hypothesis while also gathering information sufficient to determine diel feeding periodicity, daily meal, and daily ration of juvenile coho salmon and steelhead.

Methods

Subyearling coho salmon and steelhead were collected from a 200 m section of Orwell Brook, Oswego County, N.Y. The stream discharges into the Salmon River which empties into Mexico Bay in the southeastern portion of Lake Ontario. Orwell Brook is a high quality spawning and nursery stream for salmonids migrating from Lake Ontario (Johnson 1980). The 200 m stream section generally consisted of a series of pools, runs, and riffles. The surface substrate consisted of gravel and pebbles. Maximum and minimum water temperatures recorded during the study period were 21° C at 1600 h (31° C air temperature) and 16° C at 0400 h (17° C air temperature).

The study was carried out in July 1979 since previous studies had shown that subyearling coho salmon and steelhead are most abundant in Orwell Brook at this time (Johnson 1980). Maximum numbers of coho salmon and steelhead in the stream were desired in order to facilitate collections and to prevent depletion of the populations of each species. Fish were collected at 4-h intervals commencing at 0800 h on 13 July and ending at 0400 h on 14 July 1979. During the study period sunrise occurred at 0436 h and sunset at 1943 h e.s.t. A minimum of 20 individuals of each species on 13 July 1979 was collected during each 4-h interval. Fish were collected with a 3 m seine, slit, and immediately placed in 10% Formalin[1] in order to halt digestive processes. Prior to the removal of their digestive tracts all fish were weighed (grams) and measured (millimeters total length, TL). Correction factors were used to account for weight gain and length shrinkage caused by preservation (Parker 1963; Stauffer[2]). Dietary items were identified to the family level for aquatic invertebrates and to the ordinal level for terrestrial invertebrates.

Dry weight estimates were obtained for individuals of each family of aquatic prey and each order of terrestrial prey (invertebrate taxa which had no life state occurring in the aquatic environment) to determine the relative contribution of food organisms in the fishes' diet. A representative number of individuals of each prey taxa (usually 10) were used to derive a dry weight estimate. Food items were placed in small preweighed pans and then dried at 105° C for 24 h. The pans were then placed in a desiccator for 6 h, and reweighed. The dry weight of the organisms in the pan was divided by the number of individuals in the pan giving an average dry weight estimate of an individual of that taxa. Dry weight determinations were used to estimate diet composition for both coho salmon and steelhead for each 4-h interval. In addition, dry weight estimates for each taxon were summed for the 24-h period to derive an estimate of diel diet composition.

To examine diel patterns of food consumption of both coho salmon and steelhead the total dry weight of the stomach contents per dry weight of

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Stauffer, T. M. 1971. Salmon eggs as food for stream salmonids and sculpins. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1776, 10 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

the fish was plotted for each 4-h interval. Dry weight estimates for each fish were based on the entire carcass. These estimates were derived experimentally using a dry weight to wet weight conversion (21.1%) based on the combined results of 15 individuals of each species.

Daily meal and daily ration of subyearling coho salmon and steelhead were determined by summing interval values for the 24-h period. The amount of food consumed at each 4-h interval, was estimated from the Elliott and Persson (1978) formula:

$$C_t = \frac{(S_t - S_0 e^{-Rt})R_t}{1 - e^{-Rt}}$$

where C_t = amount of food consumed in t hours
S_t = mean stomach contents at the end of the interval
S_0 = mean stomach contents at the beginning of the interval
R = exponential rate of gastric evacuation in t hours.

Estimates of R were derived using available information for subyearling rainbow trout (Windell et al. 1976).

Variability in the diet of coho salmon and steelhead over the 24-h period, and diet similarity between coho salmon and steelhead between sampling periods spaced 4 h apart were examined using the overlap formula of Morisita (1959) modified by Horn (1966):

$$C_\lambda = \frac{2 \sum_{i=1}^{s} X_i \cdot Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where C_λ = overlap coefficient
s = food categories
X_i = proportion of the total diet of fish species X contributed by food category i
Y_i = proportion of the total diet of fish species Y contributed by food category i.

C_λ can range from 0, when samples contain no food in common, to 1, when there is identical representation of food between samples.

Results

A total of 130 coho salmon and 142 steelhead were examined for diet composition and feeding periodicity (Table 1). Subyearling coho salmon which emerge approximately 6 wk earlier than subyearling steelhead were substantially larger at the time of collection. Terrestrial invertebrates were the major components (51.3-62.3%) in the diurnal diet of coho salmon fry, whereas aquatic invertebrates were the major prey utilized at night (89.5-96.9%) (Table 2). Predation on terrestrial invertebrates was greatest between 1600 and 2000 h and greatest on benthic invertebrates between 2000 and 2400 h. Of the aquatic taxa immature chironomids were the most important item (17.1%) during the 24-h period although some diel variation in importance is suggested. Other less important aquatic items include adult chironomids (7.7%), caenid (7.0%), and leptophlebiid (6.8%) mayfly nymphs along with hydropsychid caddisfly larvae (6.0%). Homopterans (6.5%), dipterans (5.4%), and coleopterans (4.8%) were the major terrestrial invertebrates consumed. Overall, aquatic invertebrates composed 74.7% and terrestrial invertebrates 25.3% of the diel diet of coho salmon (Table 2).

Aquatic invertebrates were the principal food of subyearling steelhead throughout the 24-h period (Table 2). Although steelhead did not utilize terrestrial invertebrates to the extent that coho salmon did during diurnal feeding, temporal patterns in the consumption of terrestrial prey were

TABLE 1.—Number examined, mean total length (millimeters ± 95% confidence limits), mean dry weight of fish (gram) and stomach contents (milligrams), and C_λ of subyearling coho salmon and steelhead. Data are from sampling intervals spaced 4 h apart, 13-14 July 1979, in Orwell Brook, N.Y.

	Coho salmon					Steelhead			
Time	Number	Length	Weight	Stomach contents	C_λ	Number	Length	Weight	Stomach contents
0800	20	70.9±4.1	0.63	1.83	0.70	24	49.7±2.7	0.23	1.40
1200	25	66.1±5.7	.53	2.01	.53	20	55.2±2.6	.32	1.66
1600	20	62.5±5.1	.45	.90	.42	28	53.7±1.6	.30	2.58
2000	21	71.0±3.5	.68	2.65	.64	24	55.1±2.5	.32	4.26
2400	22	68.4±3.9	.58	5.80	.82	24	51.1±2.4	.25	1.45
0400	22	64.4±4.6	.49	3.77	.91	22	49.0±2.8	.22	1.08

TABLE 2.—Percentage dry weight dietary composition of subyearling coho salmon and steelhead sampled at 4-h intervals over a 24-h period, 13-14 July 1979, in Orwell Brook, N.Y.

	Coho salmon							Steelhead						
Taxon	0400	0800	1200	1600	2000	2400	24-h total	0400	0800	1200	1600	2000	2400	24-h total
Oligochaeta	—	—	—	—	—	—	—	0.21	0.70	0.25	0.15	—	—	0.19
Ostracoda	—	—	—	—	—	—	—	—	.08	—	—	—	—	.01
Hydracarina	0.05	0.92	0.48	1.59	0.32	0.07	0.31	.27	.58	.16	.67	0.59	0.55	.52
Collembola	.06	—	.56	—	.09	—	.09	1.41	.14	.67	.10	.18	—	.29
Plecoptera:														
Chloroperlidae	.88	—	—	—	—	—	.20	1.53	—	—	—	—	—	.10
Leuctridae	4.64	6.28	—	—	—	2.46	2.62	4.12	—	—	1.24	—	1.13	.69
Perlidae	5.06	—	—	—	6.24	8.28	3.23	2.02	3.82	—	6.19	.36	.60	2.30
Unidentified	.05	—	1.96	1.25	—	.15	.33	—	1.01	1.08	—	.84	—	.54
Ephemeroptera:														
Baetidae	3.95	3.88	.81	—	.55	3.50	2.77	9.69	11.27	16.11	12.30	6.53	8.31	9.93
Caenidae	.25	1.74	.28	—	—	18.10	7.03	11.01	5.04	10.46	5.21	2.48	5.88	5.35
Ephemerellidae	2.27	3.13	—	—	—	4.38	2.47	1.19	1.39	—	1.60	.83	6.30	1.63
Ephemeridae	—	—	.98	—	—	3.88	1.55	—	—	—	—	—	—	—
Heptageniidae	.27	.29	—	2.24	—	2.71	1.21	2.94	—	—	—	—	2.99	.57
Leptophlebiidae	7.53	.47	1.15	—	—	13.33	6.83	4.00	1.31	1.89	2.00	1.18	1.94	1.75
Unidentified	1.65	.89	23.32	1.99	7.42	—	4.22	—	6.59	9.62	15.52	2.50	.77	6.30
Odonata:														
Aeshnidae	—	—	—	—	—	.54	.20	—	—	—	—	—	—	—
Trichoptera:														
Glossosmatidae	.16	.58	.14	—	—	.23	.19	—	—	—	1.76	.92	2.04	.95
Helicopsychidae	—	—	—	—	.26	—	.04	.59	—	—	—	.28	—	.14
Hydropsychidae	11.77	1.77	5.60	—	.72	6.55	5.98	4.12	5.37	2.60	.71	.66	15.91	3.51
Odontoceridae	—	—	—	—	—	—	—	2.10	—	—	1.53	—	1.06	.61
Philopotamidae	2.93	—	—	—	—	.27	.76	—	—	—	—	—	—	—
Polycentropodidae	.41	—	—	—	—	—	.09	—	—	—	.23	—	—	.05
Unidentified	4.76	8.35	2.52	—	2.81	2.64	3.66	2.24	.30	—	2.48	2.32	3.80	2.30
Hemiptera:														
Velliidae	.41	—	—	—	—	—	.10	—	—	—	—	—	—	—
Megaloptera:														
Sialidae	—	1.66	—	—	—	.12	.22	—	.20	—	—	—	—	.02
Coleoptera:														
Dytiscidae	.49	—	—	2.49	1.12	—	.41	—	—	—	—	—	—	—
Elmidae	.76	.80	—	2.12	—	1.36	.86	—	1.09	—	—	—	2.06	.37
Psephenidae	.37	4.39	—	—	—	.70	.81	—	1.22	.84	.63	.48	3.70	.99
Diptera:														
Ceratopogonidae	.10	.39	—	—	—	.17	.12	—	.11	—	—	.08	.50	.22
Chironomidae, immature	27.48	12.95	3.31	7.04	3.28	22.28	17.08	26.33	25.80	20.03	8.44	20.34	20.82	18.76
Chironomidae, adult	11.76	3.50	7.55	12.34	12.34	3.35	7.67	14.16	3.40	2.85	9.06	15.96	15.45	11.10
Dixidae	—	—	—	—	—	.19	.07	—	—	—	—	—	.88	.10
Simuliidae	.41	.75	—	—	—	.61	.40	—	—	1.41	—	.15	.35	.23
Tipulidae	1.02	11.75	.02	15.15	2.59	1.01	3.04	2.89	16.19	.25	.10	1.11	.56	2.64
Gastropoda:														
Physidae	—	—	—	—	—	—	—	1.88	—	—	—	—	—	.13
Fish larvae	.65	—	—	—	—	—	.14	—	5.92	—	1.15	—	—	.95
Aquatic food total	90.14	64.49	48.68	46.21	37.74	96.88	74.70	92.70	91.53	68.22	71.79	57.79	95.60	73.24
Annelida	—	—	—	19.29	—	—	.90	—	—	—	—	—	—	—
Arachnida	.91	1.27	1.93	—	—	.26	.63	—	.75	1.47	.98	.91	—	.80
Coleoptera	2.91	5.15	3.19	.47	19.16	.19	4.82	5.30	3.83	4.29	5.27	12.07	2.64	7.05
Dermaptera	—	—	1.04	—	.98	—	.27	—	.17	.23	.06	.87	—	.35
Diptera	1.18	5.94	9.21	18.37	13.48	1.16	5.39	.88	1.36	6.58	5.82	7.15	—	4.98
Hemiptera	.93	.88	11.64	2.33	2.35	.47	2.17	1.12	.44	6.63	6.44	3.21	1.76	3.67
Homoptera	3.77	13.93	10.33	10.96	14.59	.34	6.45	—	.95	1.46	2.00	14.01	—	5.49
Hymenoptera	.16	2.89	13.98	2.37	11.70	.70	4.09	—	.97	8.93	7.64	3.99	—	4.15
Lepidoptera	—	5.45	—	—	—	—	.58	—	—	2.19	—	—	—	.27
Terrestrial food total	9.86	35.51	51.32	53.79	62.26	3.12	25.30	7.30	8.47	31.78	28.21	42.21	4.40	26.76

identical for the two species. Terrestrial prey were most important in the diurnal diet of steelhead (28.2-42.4%) whereas nocturnal feeding was almost exclusively on autochthonous prey (92.7-95.6%). Like coho salmon, peak consumption of terrestrial invertebrates by steelhead occurred from 1600 to 2000 h while peak consumption of aquatic prey was from 2000 to 2400 h. Baetid, caenid, and leptophlebiid mayfly nymphs along with immature and adult chironomids were the only aquatic prey taxa which were well represented in the diet of steelhead during each 4-h interval (Table 2).

The two species exhibited diel differences in feeding intensity (Figure 1). Coho salmon fry fed heaviest from 2000 to 2400 h, while peak feeding of steelhead trout fry occurred from 1600 to 2000 h. (The feeding intensity of steelhead fry also increased substantially from 1200 to 1600 h.) In general, the greatest variation in the amount of

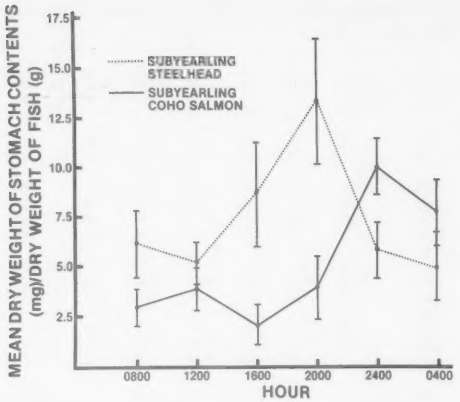

FIGURE 1.—Relative food contents (with 95% confidence limits) of subyearling coho salmon and steelhead at 4-h intervals, 13-14 July 1979, in Orwell Brook, NY.

food consumed among individual fish occurred during peak feeding periods in both species. Coho salmon appear to be primarily nocturnal feeders since their stomachs during periods of low light intensity (2000-0800 h) were much fuller ($\bar{x}$ = 6.87 mg stomach contents/g fish) than during daylight periods (0800-2000 h) ($\bar{x}$ = 3.23 mg stomach contents/g fish). Conversely, steelhead are predominately diurnal feeders. Their stomachs during the day ($\bar{x}$ = 9.03 mg stomach contents/g fish) were considerably fuller than at night ($\bar{x}$ = 5.60 mg stomach contents/g fish).

We estimated the daily meal (amount of food consumed per day) and the daily ration (amount of food consumed per day expressed as a percentage of the fish's body weight) for subyearling coho salmon and steelhead in Orwell Brook. The daily meal of coho salmon was estimated as 10.6 mg and the daily ration was 1.7% of their dry body weight. For steelhead the daily meal was estimated as 7.8 mg and the daily ration as 2.8%.

To investigate the hypothesis that the diet of coho salmon fry was more variable than that of steelhead fry over a 24-h period the overlap formula was used to compare diet similarity for each species between each 4-h sampling interval. When employing this formula, $C_\lambda \geq 0.60$ is assumed significant (Zaret and Rand 1971). Using this criterion, all possible combinations for steelhead are significant (Table 3). Only 4 of the 15 comparisons for coho salmon are significant while

TABLE 3.—Diet similarity values (C_λ) for subyearling coho salmon and steelhead between sampling periods spaced 4 h apart, 0800 h 13 July to 0400 h 14 July 1979.

		Steelhead					
		0800	1200	1600	2000	2400	0400
Coho salmon	0800		0.82	0.65	0.67	0.80	0.86
	1200	0.41		0.89	0.72	0.78	0.84
	1600	0.72	0.47		0.69	0.72	0.71
	2000	0.47	0.60	0.56		0.73	0.76
	2400	0.50	0.12	0.20	0.10		0.94
	0400	0.64	0.24	0.38	0.26	0.73	

their mean C_λ, 0.43, is much lower than that of steelhead, 0.77 (Table 4).

The diet of coho salmon and steelhead during similar 4-h intervals differed. The greatest overlap occurred between 2400 and 0400 h and the lowest from 1200 to 1600 h (Table 1). Overall, the mean diel overlap in diet between coho salmon and steelhead was significant (C_λ = 0.67).

Discussion

The results of this study support the hypothesis that the diet composition of subyearling coho salmon is more variable over a 24-h period than that of sympatric subyearling steelhead. The C_λ's for each species between different 4-h intervals (Table 4) indicate that the diet composition of coho salmon was variable, whereas that of steelhead was fairly uniform over the 24-h study period. In fact, the data show that at no time did the diet of steelhead fry (mainly aquatic invertebrates) differ substantially from diets at other 4-h intervals (e.g., all C_λ's were significant). The low similarity in the diel diet of coho salmon, as postulated, was due to the predominance of terrestrial prey in their daytime diet and predominance of aquatic prey in their nocturnal diet as C_λ's between daytime (0800-2000 h) and nocturnal (2000-0800 h) periods for coho salmon were generally the lowest ($\bar{x}$ = 0.32). Unfortunately, samples of the invertebrate drift were not taken at 4-h intervals concurrent with these fish collections. We suspect, however, that the variability in the diet of coho salmon was due to diel fluctuations in the composition of the drift, which are well documented in streams (Hynes 1970). In many streams during the summer, terrestrial invertebrates dominate the diurnal drift (Hinckley and Kennedy 1972; Johnson and Ringler 1980) while aquatic invertebrates dominate the nocturnal drift (Hynes 1970; Hinckley and Kennedy 1972). Since the diet of coho salmon fry in Orwell Brook has been shown to be significantly associated with the composition

of the drift, it is apparent why the diet composition, in synchrony with the drift, varies over a 24-h period.

Mason (1966) demonstrated nocturnal feeding activity of coho salmon fry. He attributed the night feeding habits of coho salmon to high retinal cone sensitivity, believing that it aided them in utilizing the increased drift of aquatic invertebrates during periods of low light intensity. Jenkins[3] observed that rainbow trout fed most actively at midday and that the diet at this time was composed mainly of terrestrial invertebrates which predominated in the drift. However, these fish were overyearlings, so a direct comparison with this study (fry) cannot be made since as salmonids grow older (and larger), not only do they occupy different habitats (Saunders and Smith 1962) but they also utilize different prey species (Kallenberg 1958), in addition to eating larger prey when available (Allen 1969). Tippets and Moyle (1978), however, did demonstrate that during the summer, rainbow trout fry fed predominantly on drifting invertebrates during the day in the McCloud River, Calif. In Orwell Brook in 1977, the diurnal diet of steelhead fry during the summer was found to be more closely associated with the composition of the bottom fauna rather than with the composition of the drift (Johnson and Ringler 1980). These differences in the feeding of steelhead may be due to social interaction between coho salmon and steelhead fry in Orwell Brook. In sympatry, during the summer, coho salmon occupy pools while steelhead utilize riffles (Hartman 1965; Allee 1974). In allopatry, although steelhead fry occupy both habitats, they prefer pools (Hartman 1965). If riffle versus pool occupancy influences the prey selection of coho salmon and steelhead as suggested by Johnson and Ringler (1980), the diets of steelhead fry in allopatric (predominately pools) and sympatric (predominantly riffles) situations with coho salmon may be expected to differ.

Although subyearling coho salmon actually consumed more food (10.6 mg daily meal) than subyearling steelhead (7.8 mg), because coho salmon were much heavier (Table 1), their daily ration was substantially less than steelhead (1.7 and 2.8% daily rations). Elliott and Persson (1978) suggested that, when using their formula to estimate daily food consumption, sampling intervals should be 3 h or less; larger intervals may result in inaccurate estimates. Since our sampling interval was 4 h and rates of gastric evacuation were determined from the literature (i.e., rainbow trout fry fed oligochaetes, Windell et al. 1976) using mean water temperatures (16°-21° C) for each 4-h interval, our results are, at best, rough estimates of the daily meal and daily ration of subyearling coho salmon and steelhead. However, our estimates are well within the range of juvenile sockeye salmon, *Oncorhynchus nerka*, in a lacustrine environment in Washington (Doble and Eggers 1978).

Johnson and Ringler (1980) found that the diurnal diet (0900-1500 h) of coho salmon and steelhead fry did not overlap substantially (i.e., $C_\lambda \geq 0.60$) from June through September in Orwell Brook during 1977. Interestingly, the only time that the diet of these two species did not overlap significantly in this study was during approximately the same period, 0800-1600 h (Table 1). The highest degree of overlap in the diets of coho salmon and steelhead occurred from 2000 to 0400 h when both species were feeding mainly on aquatic invertebrates. Inspection of diet overlap during twilight feeding periods (0400-0800 and 1600-2000 h) indicates significant overlap ($\bar{x} = 0.67$), which is distinctly intermediate between diurnal ($\bar{x} = 0.48$) and nocturnal ($\bar{x} = 0.87$) periods. The large diel fluctuations in diet similarity between these two species indicate that diel studies are necessary when examining aspects of their trophic ecology, at least when the species occur sympatrically. Daytime food studies could lead to the erroneous speculations that the diet of sympatric juvenile coho salmon and steelhead is not similar and that terrestrial invertebrates (at least during certain periods of the year) are the major component in the diet of coho salmon. Conversely, examination of the stomachs contents during nocturnal and crepuscular periods would indicate a great deal of similarity in diet and would not reflect the importance of allochthonous material in the daytime diet of coho salmon.

Acknowledgments

We thank N. Ringler and R. Sloan for their helpful comments on the manuscript. We also thank A. Crawford who typed the manuscript and G. Furman who prepared the figure.

[3]Jenkins, T. M., Jr. 1970. Behavior-ecology. *In* Progress in sport fishery research, p. 138-141. U.S. Fish Wildl. Serv., Bur. Sport Fish Wildl.

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THE OCCURRENCE OF *CIROLANA BOREALIS* (ISOPODA) IN THE HEARTS OF SHARKS FROM ATLANTIC COASTAL WATERS OF FLORIDA

Extensive depredation of catch triggered the closing of the only large commercial shark fishery on the Florida east coast (at Cape Canaveral) in October 1978. Shark catches had been affected throughout a 403 km stretch of nearshore waters from St. Augustine to Fort Pierce, Fla., from between 29 and 56 km offshore, at depths of 20-43 m. The organism responsible was a marine isopod, *Cirolana borealis* (Bowman[1]).

The presence of isopods (thought to be worms by the fishermen) in the heart of a shark was discovered in October 1977, when the pericardial

[1]Thomas E. Bowman, Curator, Crustacea, Department of Invertebrate Zoology, National Museum of Natural History, Washington, DC 20560, pers. commun. September 1978.

cavity of a freshly caught sandbar shark, *Carcharhinus milberti*, was accidentally opened. From January through May of 1978, increasing numbers of sandbar sharks with isopods in the gills and heart were taken. By spring, infestation was noted also in tiger sharks, *Galeocerdo cuvieri*, including one living animal in which isopods had entered the peritoneal cavity by chewing through the musculature from the right pectoral fin axil. Moderate isopod infestation of the gills was seen in one individual of a third shark species (*Sphyrna* sp.) in August 1978. Scavenging by isopods of dead sharks on setlines also increased dramatically during this period.

Shark catch declined sharply in June 1978, and up to 60% of the animals that were taken were affected by *C. borealis* (an average of 12 out of 20 sharks caught/400 hook set). The incidence rose to 100% of catch by August 1978 (an average of 22 sharks caught/400 hook set). Some of the sharks retrieved alive with isopods in their hearts showed no obvious external damage. A short pilot study in October 1978 identified the problem in the shark fishery (Bird[2]). Investigation was undertaken from June 1979 through April 1980 on the occurrence of *C. borealis*, the possible species of fishes affected, and the potential threat that the isopod posed to fisheries on the Florida Atlantic coast.

Cirolana borealis is normally a deepwater isopod. Its distribution on both sides of the Atlantic Ocean (usually at depths of 55-1,478 m) is temperature and Gulf Stream related (Richardson 1904; Schultz 1969). (One individual, a male, was noted by Menzies and Kruczynski (in press) in the Gulf of Mexico in 1967 at a depth of 55 m.) The occurrence in 1977 and 1978 off the Florida east coast in depths as shallow as 20 m appears to be a record for the species in that area. *Cirolana borealis* is eminently carnivorous, an active swimmer, and reputedly a voracious scavenger and has been noted as an occasional parasite by Sars (1899), Richardson (1905), and Halvorsen (1966). The species was recorded by Moreira and Sadowsky (1978) as an ectoparasite of *Squalus* spp. and *Raja* spp.; it was also recorded in the peritoneal cavity of *Raja* spp. *Cirolana borealis* is a morphologically capable predator. The incisors are heavily sclerotized for biting; the first three pairs of pereopods are prehensile, and the posterior pereopods are ambulatory (modified natatory).

The life cycles of most isopods are unknown (Overstreet 1978). There are few studies on the genus *Cirolana* other than those by Davis (1964), Nielsen and Stromberg (1965), Tjonneland et al. (1975), and Johnson (1976a, b). Cirolanids are not considered endoparasitic.

Methods

Fishes examined for isopods during the course of the investigation included commercially caught *Lutjanus campechanus*, *Epinephelus morio*, and *Mycteroperca microlepis* and numerous inshore and offshore species (*Dasyatis sabina*, *Raja eglanteria*, *Paralichthys lethostigma*, *Centropristis striata*, *Rhomboplites aurorubens*, *Sphyraena barracuda*, *Coryphaena hippurus*, *Haemulon plumieri*, *Euthynnus alletteratus*, *Echeneis naucrates*, *Balistes capriscus*, etc.) from fishing tournaments, shore fishermen, research vessels, and personal collection. Swordfish, *Xiphias gladius*, longline operations covering offshore areas from north of Cuba to Georgia were accompanied and their coincidental shark catches inspected for *Cirolana borealis*. Twenty-three species of sharks were examined altogether, including *Carcharhinus milberti*, *C. falciformis*, *C. limbatus*, *C. obscurus*, *Galeocerdo cuvieri*, *Sphyrna mokarran*, *Isurus oxyrinchus*, and *Ginglymostoma cirratum*.

As an adjunct to sampling, four seasonal field trails were undertaken at sites where infested sharks had been collected on setlines in 1978. Sites were "baited" for isopods with living and dead sharks placed on weighted lines and in wire cages on the bottom. Additionally, bottom samples from the area were obtained from shrimp and scallop trawlers. They were subsequently treated with rose bengal to stain organic material and screened for isopods. Faunal records and recent and historic benthic surveys were scrutinized for *Cirolana borealis* occurrence. Historic water parameters, currents, and eddies of the Florida Atlantic continental shelf were studied in regard to normal patterns and possible deviations.

Five shark samples with intact isopods were obtained. All samples were initially frozen and transferred into 10% buffered Formalin[3] on receipt. Samples 1 through 4 represented isolated

[2]Bird, P. M. 1978. Report on infestation by *Cirolana borealis* in sharks caught commercially on the Florida east coast. Fla. Sea Grant Rep. 04-8-M01-76, 14 p. Florida Sea Grant College, 2001 McCarty Hall, University of Florida, Gainesville, FL 32611.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

sections from mature sandbar sharks collected by the fishery operator[4] from various sets in winter and spring 1978; he stated the animals were alive when retrieved from the lines. The samples consisted of: sample 1—ventricle complete with atrium, conus arteriosus, and short ventral aorta section; sample 2—ventricle as above and an epidermal section from the same animal; sample 3—ventricle as above within the pericardial chamber, intact with coracoid bar and transverse septum; sample 4—two branchial arches. Sample 5 was an entire male sandbar shark, 153 cm total length (TL), collected in July 1978; it was retrieved dead from the line.

Sample 1 was subsequently examined histopathologically; the entire specimen was serially sectioned and all sections studied microscopically. The material was paraffin embedded, cut to 6-7 μm thickness, and stained with hematoxylin and eosin.

Locations of isopods within the samples, sites of attachment, evidence of feeding, and morphological distinctions were noted on initial examination. Isopods removed during subsequent dissection were measured to the nearest 0.1 mm TL; length data were classed (2 mm classes) for frequency distributions. Species identification, sex, and stage of development were determined. Isopods were transferred into 70% isopropyl alcohol after detachment.

Results

Sampling

All teleost samples were negative for *C. borealis*. Those obtained during the pilot project in October 1978 were possibly within the chronological period of isopod occurrence in nearshore waters. Occurrences of other parasites and pathologies noted in the fishes (ectoparasitic crustaceans, cestodes, monogenetic and digenetic trematodes, nematodes, infections, etc.) were within normal levels. Reports from finfish processors and historic faunal records from the area are consistent with the finding that *C. borealis* are not a problem for teleostean fishes. Elasmobranchs collected in 1979 and 1980 were also negative for the isopods. No *C. borealis* were produced by the field trials.

Bottom samples were also negative. Historic faunal surveys revealed only one recent record of *C. borealis* (provisionally identified), taken in the South Atlantic Outer Continental Shelf Benchmark Study[5] that sampled continental shelf waters from Daytona Beach, Fla., through Georgia during 1977. The season and location in which the species was collected are unknown because Benchmark faunal lists are not yet keyed for retrieval of these data. The report would place *C. borealis* in Atlantic Shelf waters within the chronological period of shark infestation by the isopod.

Water Parameters

The currents and eddies off the Florida Atlantic coast are particularly dynamic. Recent data show that deep, cold, nutrient-rich Gulf Stream waters advect onto the continental shelf many times during the year (Atkinson et al. 1978). Spin-off eddies become larger north of Jupiter, and an established, persistent upwelling feature occurs to the north of Cape Canaveral. Lee et al. (in press) noted that eddy events appear in surface waters as warm, southward-oriented extrusions of the Gulf Stream, coupled to cold, upwelled cores. They documented an unusually strong eddy in April 1977; the eddy apparently coincided with the vertical stratification of the water, which strengthened the extrusion and brought it closer to shore. Water near the bottom (63 m depth) at the shelf break from St. Augustine south had the characteristics of water from depths of from 200 to 300 m. Its Gulf Stream origin was indicated by low temperature, salinity, oxygen content, and high nutrient concentration. The eddy, which was followed by a second strong eddy event, was 225 km long (parallel to the shelf) and approximately 35 km wide; upwelling of the cold core extended into the euphotic zone (45 m depth). Lee[6] stated that the coastal area from St. Augustine to Cape Canaveral in which *C. borealis* was found in sharks in 1977 and 1978 coincided with the area influenced by the especially strong eddies in spring of 1977.

[4]Joe D. Walker, P.O. Box 356, Cape Canaveral, FL 32920.

[5]South Atlantic OCS Benchmark Program, 1977 Report. 1979. Texas Instrument Contract AA550-CT7-2, Bureau of Land Management, Vol. 1-6. Bureau of Land Management, Department of the Interior, Federal Building, New Orleans, LA 70113.

[6]Thomas N. Lee, University of Miami, Department of Energy, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, pers. commun. March 1980.

Isopods in Shark Samples

Cirolana borealis (129 total individuals) were present only in shark samples 1-5 taken in 1978. One individual of a different isopod species and one copepod were also noted in the samples. Table 1 shows the *C. borealis* population composition for each sample. No manca larvae or true juveniles were found; all had completed the molt to seven peraeonal appendages, although the last pair of pereopods were small in some individuals in the 5 mm class. No ovigerous females or females with remnant marsupia were seen. A morphological distinction between isopods was noted in that the pleopods of individuals from the conus and ventricle were consistently swollen, while about half of those from the pericardial chamber, and only two of the isopods from the gills, showed this condition. The distinction was present prior to preservation of the samples, and was possibly an osmotic response to the body fluids of the host. The distribution of *C. borealis* in the same samples pooled by site of occurrence is shown in Table 2 (note relationships between the groups, particularly in the male to female ratios).

TABLE 2.—Distribution of *Cirolana borealis* by morphological site of occurrence in pooled *Carcharhinus milberti* samples (see text) collected off the Florida Atlantic coast in 1978.

Site of occurrence	Total number	Mean TL (mm)	% Male	% Female	% undifferentiated	M/F ratio
Epidermis	2	6.6	0	100.0	0	—
Gill	41	10.1	34.1	56.2	9.7	1:1.6
Pericardial cavity	56	10.0	28.6	71.4	0	1:2.5
Ventricle	28	12.1	14.3	85.7	0	1:6
Conus arteriosus	2	15.8	0	100.0	0	—

Shark Pathology

Intact isopods in the isolated shark samples were observed free within the pericardial chamber; others had their mouthparts attached to the tissues of the atrium and ventricle. In two instances (samples 1 and 3), a single, large female was attached in the conus arteriosus, caudad-directed, anterior to the proximal semilunar valves. There was no sign of external entry into the conus or aorta. Abrasions were evident on the exterior of the ventricles, and holes extended into the lumen; large isopods with guts distended and dark from feeding were present in pockets of tissue in the ventricular walls (Figure 1). Areas of possible necrosis were noted in these samples. Much of the gill tissue was destroyed on the branchial arches, exposing the cartilaginous gill rays. The epidermal section was abraded.

Two free isopods were in the pericardial chamber of the intact shark (sample 5). A small hole (chewed) through the coracobranchial musculature led into the chamber from the left posteriormost gill. No isopods were present in the interior of the ventricle, conus, or circulatory system. The tranverse septum was entire (as was that of sample 3). Two isopods were attached at the cloacal opening, and both claspers showed minor surface injury. The hide was deeply pitted at the axil of the pectoral fins and the soft areas at the median fin bases.

Histopathology of the Shark Heart

Histopathological examination of heart sample 1 showed several *C. borealis* in the atrium near the atrioventricular opening; the adjacent endocardium and myocardium surrounding one of the organisms had areas of necrosis, determined by observation of basophilic degeneration of myocardial fibers and loss of nuclei (Figure 2). No inflammation was evident. Isopods were present in the lumen of the ventricle. Isopod mouthparts

TABLE 1.—Population composition of *Cirolana borealis* present in five *Carcharhinus milberti* samples (see text) collected off the Florida Atlantic coast in 1978.

Item	1 Heart	2 Heart and epidermis	3 Heart	4 Gill	5 Intact shark	Pooled samples
Total number	7	30	47	38	7	129
Mean TL, mm	9.0	10.8	10.9	10.5	11.3	10.9
Male/female ratio	1:2.5	1:2.3	1:5.7	1:1.8	1:0.75	1:2.7
Number of males	2	9	7	12	4	34
TL range, mm	8.6-11.5	6.6-16.7	10.9-16.3	5.8-17.7	13.6-16.0	5.8-17.7
Mean TL, mm	10.1	11.3	13.6	11.5	14.7	11.6
Number of females	5	21	40	22	3	91
TL range, mm	5.4-15.9	5.5-18.8	5.4-19.4	5.3-18.3	6.5- 9.8	5.3-19.4
Mean TL, mm	9.0	10.8	10.2	11.3	7.7	10.5
Number undifferentiated	—	—	—	4	—	4
TL range, mm	—	—	—	4.8- 5.2	—	4.8- 5.2
Mean TL, mm	—	—	—	5.05	—	5.05

FIGURE 1.—Heart of a mature sandbar shark, *Carcharhinus milberti*, taken off the Florida Atlantic coast in 1978. Note *Cirolana borealis* enpocketed in the tissues of the ventricle.

were attached to the myocardium and on the endocardial surface of the ventricle; one area of the ventricle showed signs of endocardial and myocardial degeneration. The ventricular valves appeared morphologically normal (thus, the isopod in the conus in this sample had not entered from the ventricle). Isopod mouthparts were also attached on the pericardial surface, and there were foci of mononuclear cell infiltrate in the pericardium, indicating mild inflammation.

There was remarkedly little inflammation in the heart sample, but it is well documented that sharks demonstrate a surprising lack of inflammatory response to trauma (Sigel et al. 1968; Bird 1978). The pathologist[7] dated the time of necrosis development in the shark heart muscle as 18-24 h before death, because of the lack of inflammatory cells (as would be true in a human heart). He stated the lesion should be older, however, because of the loss of nuclei from the affected muscle cells.

Discussion

The occurrence of *C. borealis* in nearshore Atlantic waters and in the hearts of sharks appeared to be an unusual phenomenon. This is indicated by the absence of the species in historic records of faunal surveys and fishery operations in the area. The large shark fishery at Salerno, Fla., operated from 1935 to 1950 with no observed depredation of catch by *C. borealis* (Springer[8]). The occurrence in 1977 and 1978 might have passed unnoticed, however, had it not been for its effect on the Cape Canaveral fishery and the serendipitous opening of the heart cavity of a shark. It is probable that the isopods were

[7]William H. Luer, Department of Pathology, Tulane University, School of Medicine, 1430 Tulane Avenue, New Orleans, LA 70112, pers. commun. April 1980.

[8]Stewart Springer, Senior Research Associate, Mote Marine Laboratory, 1600 City Island Park, Sarasota, FL 33577, pers. commun. October 1978.

FIGURE 2.—Paraffin section of *Carcharhinus milberti* atrium; hematoxylin and eosin (100×); bright field illumination. Necrosis of heart tissue demonstrated by basophilic degeneration of muscle fibers and loss of nuclei. Note *Cirolana borealis* (delineated by darkly stained exoskeleton) directly below necrotic tissue.

carried near shore by an event (or repeated events) of particularly strong upwelling, possibly the eddy of April 1977. Gulf Stream intrusions are known to exert major influences on populations of shelf biota (Atkinson et al. 1978). The isopods were not observed in the area by 1979, however, and may not have been able to survive as a species in coastal waters subject to extremes of temperature, light, and salinity, parameters which remain uniform in the deepwater environment.

Factors indicate that the *C. borealis* population in nearshore waters was aberrant: the depths were shallower than previously recorded for the species in American waters; large-scale predation on living animals was heretofore unknown. Additionally, the shark samples containing isopods were collected during three seasons (winter, spring, and summer) in 1978; and while the life cycle of *C. borealis* is unknown, it was surprising to not find a few juveniles or females with remnant marsupia in any of the samples.

Opportunistic feeding by *C. borealis* occurred when isopods and sharks were concurrently inhabiting nearshore waters. Both groups of animals may have been drawn to common areas as a response to the olfactory stimuli of baited setlines. Dead sharks on the lines were extensively scavenged, but living animals on the lines were attacked as well. Predation by isopods on active sharks on the lines would have been facilitated by the restricted avoidance capabilities of the hooked fishes. A deliberate preference by the isopods for the heart of the shark is strongly indicated, both in its predatory and scavenging activities.

The pathologies observed in the shark hearts suggest that *C. borealis* might have attacked some free ranging sharks while in nearshore waters. Shark setlines were retrieved by the fishery within 10-12 h of set because prompt recovery of catch was essential in order to maintain the quality of shark meat marketed for human consumption (Walker[9]). Yet, necrosis in heart sample 1 developed at least 18-24 h prior to the death of the

[9]Joe D. Walker, P.O. Box 356, Cape Canaveral, FL 32920, pers. commun. October 1978.

animal and perhaps longer (as indicated by the loss of nuclei in the affected muscle cells). Also, additional time would have been required for the isopod to penetrate the body wall of the shark and into the heart, and for the heart tissue to become necrotic. The disparity between the number of hours the shark could have been on the line and the length of isopod residence time in the heart muscle as shown by the well-developed necrosis would, therefore, indicate that the shark was attacked by *C. borealis* before it was hooked. Field tests in 1979 and 1980 could not, unfortunately, resolve this possibility (because *C. borealis* was not found in nearshore waters by that time) and it must remain speculative.

There is no evidence that *C. borealis* contributed to the sudden decline in shark catch in 1978, although it certainly affected utilization of catch adversely. A coincident decline in commercial catches of snapper and grouper that occurred in the area also appears unrelated to the isopods per se, particularly as no association was noted between *C. borealis* and teleosts in regard to catch depredation or predation. Probabilities are strong, however, that populations of sharks, teleosts, and isopods were all influenced by common water parameters. Upwellings have historically been associated with declines in fish catch (Jones et al.[10]) and were shown by George and Staiger[11] to be dominant in inducing shifts in benthic invertebrate and demersal fish populations in the South Atlantic Bight.

The Cape Canaveral shark fishery might not have closed in 1978 had the nature of the isopod problem been known at that time. The operator thought the shark flesh was contaminated by the isopods and was afraid to sell it, thus needlessly lost his profitable market for the meat. This, combined with reduced profits from the pitted hides and the decline in shark catch, caused undue financial hardship. The encounter with a totally new problem, of an unknown future duration, doubtlessly contributed to the disillusionment of the operator. Occasional occurrences of *C. borealis* in shallow waters should not be considered a deterrent to the establishment of commercial shark fishing operations in Florida, however. The phenomenon, if it recurs, should be of comparatively short duration; knowledge of this should aid fisheries to budget realistically during the interim. Isopods in sharks do not constitute a hazard to human health and their presence does not render shark flesh unmarketable. More frequent collection of setlines and experimental sets to define areas of less isopod prevalence would help alleviate problems of shark fisheries during possible future occurrences of *C. borealis* in nearshore waters.

[10]Jones, R., R. Gilmore, Jr., G. Kulczycki, and W. Magley. 1975. Studies of the fishes of the Indian River region. *In* Indian River Study, Harbor Branch Consortium, Annual Rep., 1973-74, Vol. 1, p. 110-183. Harbor Branch Consortium, North Old Dixie Highway, RFD 1, Box 196, Fort Pierce, FL 33450.

[11]George, R., and J. Staiger. 1979. Epifauna: benthic invertebrate and demersal fish population of the South Atlantic/Georgia Bight. *In* South Atlantic OCS Benchmark Program, 1977 Report, Vol. 3, p. 237-279 (see footnote 5).

Acknowledgments

This research was funded by the Florida Sea Grant College with support from the National Oceanic and Atmospheric Administration, Office of Sea Grant, U.S. Department of Commerce, #04-8-M01-76. I greatly appreciate the enthusiastic help in the field given by my student research assistants and the support from Sea Grant Agent Joe Halusky. Special thanks are extended to William Luer for his efforts in histological examinations and to Thiele Wetzel for his great contribution of time, effort, and boat facilities. The aid from William Tiffany in evaluating histopathological results is deeply appreciated.

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A FLUSHING-CORING DEVICE FOR COLLECTING DEEP-BURROWING INFAUNAL BIVALVES IN INTERTIDAL SAND

In planning a study on the population dynamics and annual secondary production of deep-burrowing infaunal bivalves, a device was required which could take samples in shallow intertidal sand. Though many grabs or coring devices described in the literature (Brett 1964; Hopkins 1964; Maitland 1969; Kajak 1971) might have been suitable for taking short cores (20-30 cm deep) in intertidal or even subtidal areas, none were found suitable for taking large numbers of quantitative samples to a depth of 65-70 cm below the sediment surface. A device similar to one described by Van Arkel and Mulder (1975) was built to achieve this goal.

Materials

The device (Figure 1) was built according to the specifications outlined in Table 1. All materials are obtainable from either hardware or plumbing supply houses and are interconnected using polyvinyl chloride (PVC) cement, nuts, and bolts.

Operation

When intertidal samples are taken, the site is visited at high tide or when the water over the site

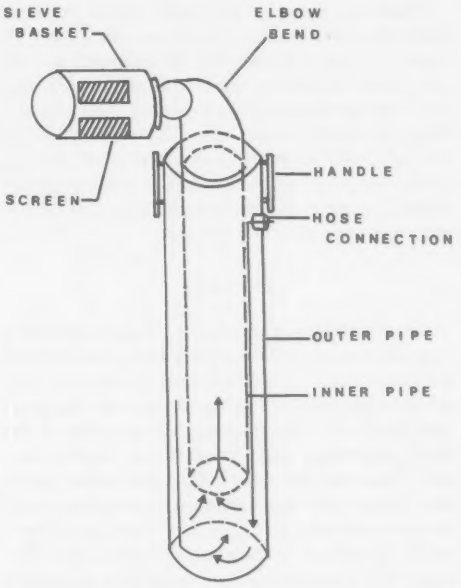

FIGURE 1.—Flushing-coring sampler. Arrows indicate direction of waterflow. Centrifugal water pump, gasoline engine, and water hoses are not shown.

TABLE 1.—Dimensions and materials used in the construction of the flushing-coring sampling system.

Item	Dimension (cm)		Material
	Diameter	Length	
Inner pipe	10.2	100.0	Polyvinyl chloride
Outer pipe	16.0	115.0	Polyvinyl chloride
Hose connection to sampler	5.1	5.1	Polyvinyl chloride
Elbow bend	10.2	—	Polyvinyl chloride
Sieve basket	16.0	30.0	Polyvinyl chloride
Side handles	2.54	20.3	Aluminum
Screen mesh (2 per sieve basket)	—	12.7	Aluminum
Hose (pump[1] to sampler)	5.1	1,000.0	Plastic
Hose (water supply to pump[1])	5.1	610.0	Heavy plastic

[1]High-pressure (22 m^3/h) water pump and 3-hp gasoline engine.

is at least deep enough to allow the pump intake hose to be submerged. The device may also be operated on exposed tidal flats if a water supply is within reach of the intake hose. The small screen over the end of the intake hose prevents debris from entering the water pumping system.

The boat is anchored and the sampling device lowered over the side and pushed several centimeters into the sediment prior to starting the pump. The operator may choose to stand in the water with waders in areas where currents and wind cause the boat to move a great deal resulting in an unstable work platform.

When the pump is activated, water is forced down the space between the inner and outer PVC pipes, forcing a suspension of sediment and all associated organisms up the smaller inner pipe and into the attached sieve basket. The operator forces the device down into the sediment to the desired depth, then the pump is shut off. At this point, the sieve basket contains all organisms and objects too large to pass through the screen. Most sediment washes easily through.

Discussion

After collecting more than 2,000 samples over a 1-yr period, no problems have been encountered with the system. A 2.5 mm mesh screen was used on the sieve basket. As the device was designed specifically to take quantitative samples of the deep-burrowing, stout razor clam, *Tagelus plebeius* Solander, for a secondary production study, the 2.5 mm mesh was adequate for sampling small bivalves and adults. Collections were made from small aluminum or fiber glass boats (3.8-4.9 m long). The system was also tested at a beach site where the water pump was placed on the shore while the operator carried the sampler into adjacent intertidal waters. Though possible, this method lacks the mobility of sampling from a boat.

Most bivalves were recovered in an undamaged condition (Table 2). In no case was a bivalve recovered with a shell broken such that shell length could not be measured, though in some specimens, small breaks in the shell allowed body fluids to escape resulting in a specimen unsuitable for an accurate biomass determination. The soft shell clam, *Mya arenaria*, and the stout razor clam have thin gaping shells that are much more susceptible to damage than the hard clam, *Mercenaria mercenaria*. Van Arkel and Mulder (1975) reported that damage to small polychaete worms was no more than if a hand corer and ordinary sieve had been used. Polychaetes were not specifically examined for damage in the present study. Many were collected in the sieve basket and though some were obviously broken, most were not.

TABLE 2.—Condition of bivalves recovered in 1,575 separate samples by the flushing-coring device.

Species	Collected (no.)	Broken[1] (no.)	Broken (%)
Tagelus plebeius	1,479	186	13
Mya arenaria	513	45	9
Mercenaria mercenaria	36	0	0
Ensis directus	3	0	0
Total bivalves	2,031	231	11

[1]Any break in the shell, no matter how small, that might allow loss of body fluids.

The maximum shell lengths (largest external dimension of the shell) of the collected specimens were 10.4, 9.15, 10.2, and 10.8 cm for *M. mercenaria*, *T. plebeius*, *Mya arenaria*, and *Ensis directus*, respectively. The heaviest bivalve, *Mercenaria mercenaria*, was estimated to weigh 200-300 g. Several of the large *M. mercenaria* were placed in the sediment and repeatedly "sampled" from the sand flat to the sieve basket to test the lifting capability of the system. The test specimens were always easily raised.

Direct visual observations in shallow water indicate that no water or sediment escapes under the outer pipe when in operation. The outer pipe has a large diameter (16 cm), thus the surface area of a single sample (0.02 m^2) is quite large.

The main advantages of this system are its mobility (as mobile as a small, shallow-draft boat) combined with the fact that deep cores can be taken and sieved in one fast process. Samples can routinely be taken to a depth of 65-70 cm below the sediment surface. Organisms can be immediately placed in storage containers, ready to be processed upon returning to the laboratory. The use of PVC parts and removable sieve basket screens allows the investigator to build and modify the device to one's own specifications depending on the particular goals of the study.

Acknowledgments

I wish to thank Czeslaw A. Bartusiak for providing assistance and a workshop in which to construct the device. This project was supported in part by an Old Dominion University, Institute of Oceanography (Norfolk, Va.), Graduate Fellowship.

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ERRATA

Fishery Bulletin, Vol. 79, No. 1

Gooding, Reginald M., William H. Neill, and Andrew E. Dizon, "Respiration rates and low-oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*," p. 31-48.

1) Page 31, Abstract, first paragraph, line 9, correct to read:
independent of weight effects)—$\log_{10}\dot{V}O_2 = -1.20 + 0.19 \log_{10}W + 0.21\ S$. However, laboratory fish
2) Page 37, left column, first paragraph, lines 13 and 15, correct to read:
(grams) = $-2.657 + 3.532 \log L$ (centimeters);
$3.368 \log L$ (centimeters) ($\log = \log_{10}$). This com-
3) Page 37, right column, the equation, correct to read:
$$S = 3.55 - 0.53 \log \overline{W} - 0.02t - 0.04 \cdot k$$
4) Page 37, right column, line above the heading Respiration Rate, correct to read:
$\log \overline{W}$ (Figure 2).
5) Page 38, right column, lines 1 and 6, correct to read:
body weight (Figure 2): $S = 3.14 - 0.53 \log \overline{W}$.
left with $\log \dot{V}_{O_2} = -0.54 + 0.08 \log \overline{W}$. Thus,
6) Page 43, left column, second paragraph, line 4, correct to read:
relation $S = 3.14 - 0.53 \log \overline{W}$. Magnuson
7) Page 44, left column, line 2, correct to read:
(Figure 9).

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